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Abstract

The eelpout genera *Gymnelus* and *Gymnelopsis* are revised on the basis of most of the world's preserved material. Of the four nominal species of *Gymnelus*, three are recognized: *G. viridis*, with *G. bilabrus* a synonym, *G. retrodorsalis* and *G. hemifasciatus*. The nominal genus *Commandorella,* established for a single species, *C. popovi*, is a junior synonym of *Gymnelus*; the species is valid and redescribed on the basis of 97 specimens. *Nemalycodes grigorjewi* Herzenstein is removed from synonymy with *Gymnelus viridis* and designated *nomen dubium*. Three previously described species of *Gymnelopsis* are recognized: *G. ocellatus*, *G. brashnikovi* and *G. ochotensis*. Two nominal genera, *Derjuginia* Popov and *Gengea* Katayama, established for the latter species, are placed in synonymy with *Gymnelopsis*. Two new species, ***Gymnelus pauciporus*** and ***Gymnelopsis brevifenestratus***, are described from the western North Pacific.

Résumé

Les genres de lycodes *Gymnelus* et *Gymnelopsis* sont révisés à partir de la majorité des spécimens de collection conservés dans le monde. Des quatre espèces nominales de *Gymnelus*, trois sont reconnues : *G. viridis* — avec le synonyme *G. bilabrus* —, *G. retrodorsalis* et *G. hemifasciatus*. Le genre nominal *Commandorella*, établi pour une seule espèce (*C. popovi*), est un synonyme mineur de *Gymnelus*; l'espèce est reconnue et redécrite d'après 97 spécimens. *Nemalycodes grigorjewi* Herzenstein n'est plus considéré comme synonyme de *Gymnelus viridis* mais est désigné *nomen dubium*. Trois espèces précédemment décrites sont reconnues : *Gymnelopsis ocellatus*, *G. brashnikovi* et *G. ochotensis*. Deux genres nominaux, *Derjuginia* Popov et *Gengea* Katayama, établis pour les espèces qui viennent d'être mentionnées, deviennent des synonymes de *Gymnelopsis*. Deux nouvelles espèces, ***Gymnelus pauciporus*** et ***Gymnelopsis brevifenestratus***, sont décrites comme indigènes dans le Nord du Pacifique occidental.

Introduction

The zoarcid genera *Gymnelus* and *Gymnelopsis* comprise a group of benthic fishes of arctic and boreal seas. They are diminutive eelpouts whose habitats range from rocky intertidal kelp stands to mud, sand and gravel bottoms of the upper continental slope. The species of *Gymnelus* have been described or listed from the Okhotsk, Bering and all Arctic seas except the White and the Norwegian (summarized in Shmidt, 1950; Andriashev, 1954; pers. obser). *Gymnelopsis* species are known only from the Japan and Okhotsk seas.

Shmidt (1950), Andriashev (1954) and Lindberg (1971, 1974) placed *Gymnelus* and *Gymnelopsis* (and synonyms) in subfamily Gymnelinae, but without comparative analysis. The results of this study indicate the subfamily should be expanded to include similar forms known only from the western North Pacific, however, the resolution of zoarcid relationships awaits further study (Peden and Anderson, 1978; Anderson and Hubbs, 1981).

Considerable taxonomic confusion has plagued the literature on these genera since the early nineteenth century. Most of the confusion has resulted from the use of characters which were not diagnostic; these were usually variable, age-dependent measurements or colouration. Several reliable characters are revealed only through cleared and stained preparations or radiographs and statistical comparison of large samples, techniques unknown in the early literature. Also, due to the widely scattered, relevant museum material, there has been no published comparison of American Arctic, Euro-Siberian and North Pacific forms. I have had the opportunity to study most of the preserved specimens of *Gymnelus* and *Gymnelopsis* in the world including all extant types except *Gengea japonica*, and this paper is a result of that comparison. Many very old, historically important collections have never been critically examined before and I was able to successfully compare most of these with recent specimens taken chiefly in the Canadian and Siberian Arctic and the Okhotsk Sea. As a contribution to the clarification of systematic problems within these two genera, I redescribe all species, list synonymies, provide a key, distributional maps and illustrations to facilitate identification and present an osteological description of *Gymnelus viridis* and compare this species to some other gymneline eelpouts.

Historical Account

The Danish monk, Otto Fabricius, published in his *magnum opus* Fauna Groenlandica (1780) a description of the common littoral eelpout of Greenland which he named *Ophidium viride*, alluding to its greenish colour. Lacépède (1800), despite knowledge of Fabricius' work, applied the name *O. unernak* to the species based on its Inuit name. Bloch and Schneider (1801) under the name *Ophidium chinense* (northern Europe) seem to have applied the description of their subsequent account (*O. viride*) to their plate 90 (mistakenly labelled *O. imberbi*), which is a fair rendition of the Arctic dwelling *Gymnelus retrodorsalis* Le Danois. Pennant (1812) copied this figure, terming it "Beardless Ophidium," a name Yarrell (1841, 1859) applied to *Pholis gunellus* (as *O. imberbe*).

Reinhardt (1834, 1837a) removed *O. viride* from the *Ophidium* conglomerate and established *Gymnelus* for it. Later (Reinhardt, 1837b, 1838) he improperly emended the spelling to *Gymnelis*, the correct grammatical construction, and this spelling has been accepted and used by most authors since. Lay and Bennett (1839) described another species, *O. stigma*, from Alaska, apparently erroneously stating their single specimen possessed scales, but it was not preserved. The names *Gymnelis viridis* or *Ophidium stigma* were applied to specimens collected by European, Russian and North American explorers and scientists throughout the remainder of the nineteenth century, although other, unrecognized species were taken often. During that century five names appeared in the literature for *G. viridis*, compounding the confusion (*O. stigma* Lay and Bennett, 1839, from Arctic Alaska; *Gymnelis pictus* Günther, 1862, from Greenland; *Gymnelichtys antarcticus* Fischer, 1885, erroneously stated to be from the Antarctic; *Cepolophis viridis* Kaup, 1856a, new name and *Maynea stigma* Jordan and Evermann, 1896, new name). *Nemalycodes grigorjewi* Herzenstein, 1896, described from Novaya

Zemlya, was placed in the synonymy of *G. viridis* by Knipovich (Knipowitsch) (1901) and Andriashev (1954).

Descriptive notes and the appearance in species lists prepared from Arctic collections compose most of the latter nineteenth century literature on *Gymnelus*. Richardson (1855) gave a very detailed description of *G. viridis* and commented on the uncertain status of *Ophidium stigma*. Kaup (1856b) gave a brief description of one specimen of *G. viridis* and later, despite knowledge of Reinhardt's work, introduced the genus *Cepolophis* (sometimes spelled *Cepholophis*) for this species and *Pholis gunnellus* (Kaup, 1856a). Krøyer (1862) classified 33 colour varieties of Greenland *G. viridis*, possibly including some *G. retrodorsalis*. Other confusions of *G. retrodorsalis* with *G. viridis* by nineteenth century authors include specimens reported by Malmgren (1865) from Spitsbergen, by Collett (1880) from collections of the Norwegian North Atlantic Expedition in the Greenland and Barents seas and by Knipovich (1907, 1908) from collections of the Russian Polar Voyages of Baron E.V. Toll and the Russian Arctic Institute's ANDREI PERVOZVANNIY, primarily in the Barents and Kara seas.

During the first half of the twentieth century, additional species of *Gymnelus* were discovered and described. Rutter's (1899) collections of *G. popovi* on Kodiak Island, Alaska, in 1897 were recognized by Charles H. Gilbert of Stanford University as a species distinct from *G. viridis* and were given a manuscript name, though he never published. A.M. Popov of the Zoological Institute in Leningrad likewise recognized the species as new from Soviet collections in the Commander Islands, Bering Sea, but also never published. The earliest collection of *G. popovi* I was able to locate was made by Lucien Turner of the U.S. Fish Commission on Unalaska Island (Aleutian Islands) in 1878. The species was finally described as *Commandorella popovi* by Taranets and Andriashev (1935), distinguished from *Gymnelus* on the basis of a few minor characters.

The first deepwater, high Arctic *Gymnelus* species, and the second to be described in the genus, was named *G. retrodorsalis* by Le Danois (1913), alluding to the far posterior dorsal fin origin. It was described from a single, unregistered specimen of which no subsequent record was found. Although a distinctive and relatively abundant species in polar collections and apparently seen by early nineteenth century ichthyologists, *G. retrodorsalis* went unrecognized by ichthyologists, particularly Adolph Jensen, a zoarcid student. Finally, Andriashev (1954) provided an adequate description and differentiated *G. retrodorsalis* from *G. viridis*, although a few specimens of *G. hemifascitus*, described by him earlier, (Andriashev, 1937) were confused with both species.

Soldatov and Lindberg (1930) gave a description and table of measurements of three specimens of a *Gymnelus* from the Okhotsk Sea. Although these specimens represented a distinct species (*G. hemifasciatus*), they could not distinguish them from *G. viridis* (or others) from Soviet Arctic collections. They referred to the presumed isolated Okhotsk population as *Gymnelis viridis* morpha *ochotensis*. Andriashev (1937) named *Gymnelus hemifasciatus* from two Bering Sea specimens, but did not comment on Soldatov and Lindberg's fish. In this work, he described *Gymnelus bilabrus* as well, based on two specimens of *G. viridis* with their upper lips more strongly adnate to the snout than other specimens. The first collection of *G. hemifasciatus* I found was made at Novaya Zemlya in 1883 (ZIL 8513). Only four other specimens of the adnate-lipped *G. viridis* were found.

Soldatov (1922) described *Gymnelopsis ocellatus* and *G. brashnikovi* from the Okhotsk Sea and allied them with the scaleless Arctic species. He established the new genus solely on the basis of the presence of scales on the tail. Shmidt (1950) designated another of A.M. Popov's unpublished species, *Gymnelopsis guntheri*, as a subspecies of *G. ocellatus* on the basis of some morphometric characters and shorther lateral line. In this work, Shmidt followed Taranets (1937) in placing *Gymnelopsis brashnikovi* in the synonymy of *G. ocellatus*, which he justified by the single specimen's small size and less complete scale cover. Lindberg and Krasyukova (1975), however, resurrected *G. brashnikovi* on the basis of its more extensive scalation, greater number of dorsal fin rays,* lack of ocelli in the dorsal fin

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*In the text of their account Lindberg and Krasyukova (1975) state *Gymnelopsis brashnikovi* has fewer dorsal fin rays, although Soldatov (1922) listed and distinguished the species by its greater number of rays. In fact, for the same specimen, ZIL 13029 (holotype), they give two different counts, 110 and 104–105 dorsal rays without defining their method of counting. No significant differences exist in vertebral or fin ray counts for the two species. See Table 3 for redetermined counts.

(although Shmidt, 1950, states feeble traces of ocelli were present, I found none) and absence of caniniform teeth on the vomer, all characters given by Soldatov (1922). Lindberg and Krasyukova supplemented their decision by showing from radiographs that the origin of the dorsal fin in *G. brashnikovi* is above vertebrae 8–9, while in *G. ocellatus* it is above vertebrae 4–5 and that *G. brashnikovi* has a shorter preanal length and possesses well developed suborbital pores. Lindberg and Krasyukova erroneously stated *G. brashnikovi* had six branchiostegal rays and did not note other differences in the cephalic lateralis pore pattern which exist in the two species.

Popov (1931) described *Derjuginia ochotensis* from a single young specimen taken in the Okhotsk Sea. Although this was another scaled species allied to the Arctic *Gymnelus*, Popov presented no comparative analysis for establishing a new genus distinct from *Gymnelopsis*. Katayama (1941) established *Gengea japonica* for this species on the basis of its more extensive scalation and more posterior dorsal fin origin than *Gymnelopsis*, apparently unaware of Popov's paper. Shmidt (1950) supplemented Popov's brief description from additional material and justified separate generic status for the species on the basis of the greater scale cover, more complete lateral line and some morphometric features. Lindberg and Krasyukova (1975) reviewed the characters given by Katayama (1941, 1943) for *Gengea japonica* and distinguished it from *Gymnelopsis ocellatus* on the basis of five character states, but were unaware of their Soviet colleague's literature on the species.

Methods and Materials

Measurements were made with ocular micrometer or dial calipers to the nearest 0.1 mm. Osteological observations were made on cleared and alcian blue-alizarin red stained specimens (Taylor and Van Dyke, ms.) and drawings made with the aid of a camera lucida. Definitions and methods generally follow those of Peden and Anderson (1978) and Gosztonyi (1977) with the following exceptions and additions (in cases of contradiction, methods follow Peden and Anderson, except for head pore terminology): caudal fin rays are those associated with the epural(s) and hypurals; all others are either dorsal or anal rays; these were counted from radiographs. Measurements including tip of snout were measured from the fleshy snout tip and do not include upper lip. Gill slit length was measured from upper, anterior corner of opercular lobe to lower corner in a straight line. Pectoral B/L ratio refers to the length of the pectoral fin base, measured from upper to lower ray, as percent of the longest pectoral ray. Cephalic lateralis pore terminology follows that of Fedorov (1976) and Gosztonyi (1977) except that their mandibular and preopercular pore counts are combined into a preoperculomandibular count since the canals are continuous in *Gymnelus*. In some adult specimens two lateralis pores formed in close proximity where usually one was present. In other adults, pores were actually missing, apparently having never formed. In some species a third supraorbital pore develops between the eyes and is termed the interorbital pore. In a few species the first few dorsal fin pterygiophores (interneuralia) bear no corresponding fin ray and these are termed free pterygiophores.

Specimens examined in this study are deposited in the collections of the University of Alaska, Fairbanks (UA); University of British Columbia, Vancouver (BC); British Columbia Provincial Museum, Victoria (BCPM); University of Washington, Seattle (UW); California Academy of Sciences, San Francisco (CAS); Stanford University (SU; now housed at CAS); University of Wisconsin, Madison (UWZ); University of Michigan, Ann Arbor (UMMZ); Biological Station, Fisheries and Oceans Canada, St. John's, Newfoundland (FOCN); National Museum of Natural Sciences, National Museums of Canada, Ottawa (NMC); National Museum of Natural History, Washington, D.C. (USNM); British Museum (Natural History), London (BMNH); Institute für Seefischerei, Hamburg (ISH); Zoological Museum, University of Copenhagen (ZMUC); Zoological Museum, University of Oslo (ZMUO); Zoological Institute, Academy of Sciences, USSR, Leningrad (ZIL); Museum National d'Histoire Naturelle, Paris (MNHN).

Abbreviations for anatomical terms used in the text figures are given in Appendix I. Specimens used in the osteological analysis are listed in Appendix II, as are collection data for all other specimens examined in this study. Specific geographical areas are combined for each species; their museum number and number of individuals are given, followed by latitude and longitude, when known, depth in meters and date, or other pertinent data. A listing of specimens for which data is probably erroneous or is substantially lacking follows after each species' listing. In the interest of brevity, and because complete data is often lacking for older collections, sex, length, gear employed and collector are usually not given, but a summary of the more important collections follows.

Specimens from Greenland and the adjacent North Atlantic deposited in ZMUC were studied and the earliest of these include specimens Reinhardt (1834, 1837a, 1837b, 1838) used to establish *Gymnelus*, collected in southwestern Greenland between 1829 and 1833. Explorations in Greenland waters by Fridtjof Nansen in 1901 aboard the FRAM produced a few *Gymnelus* housed at ZMUO. Recent collection by the FFS ANTON DOHRN and FFS WALTHER HERWIG of the Federal Republic of Germany in southwestern Greenland are deposited with ISH.

Specimens from several early nineteenth century expeditions in Canadian waters were examined at BMNH dating to those of Captain Sir James C. Ross (1828–1833). The vast majority of Canadian collections examined are deposited at NMC, most of it collected by the MV CALANUS and MV SALVELINUS of the Arctic Biological Station, Fisheries and Oceans Canada after 1960.

Euro-Siberian Arctic expeditions by several countries captured *Gymnelus* specimens frequently and museum specimens date from the late nineteenth century from the Atlantic Arctic. Fish from the Norwegian North Atlantic Expedition (1876–1878) reported by Collett (1880) from Spitsbergen and Jan Mayen were examined at ZMUO. Specimens from the Kara Sea collected by the Danish vessel DIJMPHNA in 1882–1883 were studied at ZMUC. The Zoological Polar Expedition of A.E. Nordenskiöld in 1900 aboard the VEGA produced a few *Gymnelus* specimens from Spitsbergen, now housed at USNM and Uppsala University. All extant specimens of *Gymnelus* studied by N.M. Knipovich (1907, 1908) were re-examined at ZIL from the Russian "Expedition for Scientific Fishery Investigation of the Murmansk Coast," collected by the ANDREI PERVOZVANNIY in the Barents and Kara seas (1899–1903) and those taken by Baron E.V. Toll and A. Birula between 1900 and 1903 aboard the ZARYA in the Barents, Kara and Laptev seas. A few specimens were found that A.M. Popov (1933) studied from the "Hydrographical Expedition to the Arctic Sea" taken by the TAYMYR and VAIGACH in the Laptev, East Siberian and Chukchi seas (1913-1914). Many other *Gymnelus* specimens were examined from the Leningrad collection taken by the Soviet Arctic Institute between 1930 and 1939 from all Soviet Arctic seas (except White) by Gorbunov, Vagin, Ushakov, Papanin and Shirshov chiefly aboard the vessels SADKO, SEDOV, KRASIN, RUSANOV and SIBIRYAKOV.

Gymnelus and *Gymnelopsis* specimens from the Soviet Far-Eastern seas now housed at ZIL and USNM were examined, the earliest of which date from the end of the nineteenth century. Collections made by V.K. Brazhnikov in 1899 off the Amur River mouth in the Okhotsk Sea contain the earliest extant specimens I was able to find from the Far-East. Most specimens from the Okhotsk Sea collected during the Eastern Ocean Hydrographical Expedition (1907–1913) by F.A. Derbek and others aboard the OKHOTSK were studied. Other early Russian collections that produced *Gymnelus* and *Gymnelopsis* made by V. Soldatov and M. Pavlenko on the LEITENANT DYDYMOV and E. Suvorov and P. Ushakov were discussed by Shmidt (1950). Small collections of *Gymnelus* made by the Pacific Ocean Scientific Institute of Commercial Fisheries (TINRO) with the vessels KRASNOARMEYETS and DAL'NEVOSTOCHNYKH in 1932 and 1933 were described by Andriashev (1937) and all these were examined. The expeditions of the All-Union Research Institute for Fisheries and Oceanography (VNIRO) between 1949 and 1956 with the vessel VITYAZ' in the Japan, Okhotsk and Bering seas collected numerous *Gymnelus* and *Gymnelopsis* specimens, most of which were examined in some detail, however, several of these VITYAZ' and early TINRO specimens require re-examination.

American collections of *Gymnelus* in the North Pacific date from the Bering Sea cruises of the ALBATROSS in 1890-1891. This vessel made several dredge hauls in the Okhotsk and Japan seas in 1906 that produced *Gymnelopsis* as well. More recently, cruises for Oregon State University and the University of Alaska by the ALPHA HELIX in the Bering and Chukchi seas in 1973 yielded several specimens. Shore collections in the Aleutian Islands produced the vast majority of *Gymnelus popovi* examined. The larger collections were made by C.L. Hubbs in 1939 (housed at UMMZ), by J. Hubbard and W. Reeder in 1962 (housed at UWZ) and by N. Wilimovsky and A. Peden in 1961 and 1962 (housed at BC).

Osteology

Osteology of *Gymnelus viridis*
Neurocranium and Ethmoid Region
Figures 1, 2

The bones of the neurocranium are well ossified and bear the supraorbital, postorbital and occipital canals of the lateralis system in tubular channels or over their surfaces. The sclerotics, basisphenoid, intercalars and dermosphenotics are absent.

Mesethmoid. The mesethmoid has a thin-walled, cup-shaped anterior section with low, rounded ridges along the anterolateral margin for ligaments that attach the maxilla and palatine bones to the neurocranium. Dorsoposteriorly the mesethmoid tapers to a thin strut for articulation with the frontals, which form a common groove between them for its reception. Ethmoid cartilage fills the anterior cup-shaped depression and this articulates with a median ridge of the parasphenoid and the lateral walls of the vomer. The only bones the mesethmoid contacts are the frontals posteriorly. The posterior margin of the ethmoid cartilage forms a deep notch in the anterior myodome (Fig. 1B).

Lateral ethmoid. Each lateral ethmoid forms the anterior border of the orbit. The posteromesial surface articulates with the frontal in a shallow groove and lies close to each side of the mesethmoid. Each lateral ethmoid has a wide, thick, decurved wing which is variably sculptured along its anterior edge. A deep, mesial channel for the passage of the supraorbital lateralis canal is formed anteriorly adjacent to the mesethmoid. A large foramen pierces the center of the mesial channel directly below the anteriormost tip of the frontals. A deep fossa for attachment of ligaments connecting the palatines is formed on the ventral surface of each lateral ethmoid.

Nasal bones. The nasal bones are thin, irregularly shaped tubes passing the supraorbital canal. The anterior opening lies close to the first supraorbital pore. The anterior tip of the bone lies above a notch formed by the external surface of the ascending process of the premaxilla and the body of the premaxilla. The posterior end lies just anterior to the mesial trough of the lateral ethmoid.

Vomer. The vomer is anteriorly rounded in both lateral and dorsal aspect. The ventral surface usually bears 4–6 teeth. A deep, concave fossa forms dorsally into which the anterior end of the parasphenoid fits. Posteriorly the vomer tapers to a sharp tip and becomes dorsoventrally flattened along the articular surface of the parasphenoid. A narrow space of ethmoid cartilage separates the vomer and mesethmoid.

Parasphenoid. The anterior end of the parasphenoid has a narrow dorsomedial ridge for articulation with ethmoid cartilage. The ventral surface of the anterior end has a deep, V-shaped groove into which the posterior strut of the vomer fits. At its midlength the parasphenoid wing forms two rami, one directed anterodorsally, the other posterodorsally. The anterior ramus extends upward about half the height of the trigeminofacialis foramen and has a moderately deep trough cut in its posterodorsal edge for reception of the descending wing of the frontal and pterosphenoid. The posterior ramus of the wing is low and interdigitates with the prootic. Articulation with the basioccipital posteriorly is just in front of the prootic-basioccipital juncture.

Frontal. The frontals are the largest bones of the skull, forming the roof of the orbit and anterior half of the back of the head. Each bone has a shallow, external notch anteriorly for articulation with the lateral ethmoids and a deep, mesial groove which receives the supraorbital lateralis canal from the lateral ethmoids. This branch of the lateralis system forms a tube through the bone and opens laterally where the frontal is widest. At this point, a thickened dermal tube is formed leading to the first postorbital lateralis pore. Just posterior to this another foramen is formed similarly opening to the second postorbital pore. Posterior to this area the canal passes above the sphenotic but re-enters bone at the anterior tip of the pterotic. The frontal forms a shallow notch for articulation with the sphenotic. The posterior margin of the frontal is irregularly shaped and lies under the parietal and above the anterior blade of the supraoccipital. The descending process of the frontal articulates with the pterosphenoid and parasphenoid wing.

Pterosphenoid. The pterosphenoid forms the anterior border of the trigeminofacialis foramen

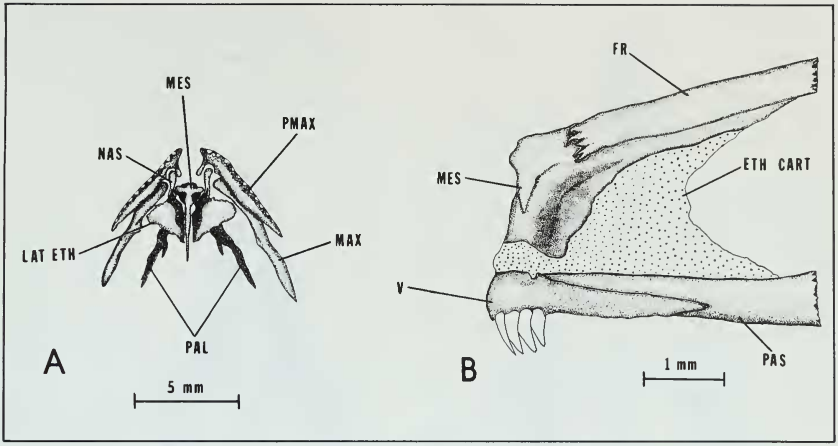

Figure 1. *Gymnelus viridis*: A) dorsal view of bones of the ethmoid region of NMC 62-379, frontals and parasphenoid not shown; B) lateral view of ethmoid region of NMC 77-1259, lateral bones not shown.

in conjunction with the parasphenoid wing with which it articulates. It is a thin bone and articulates dorsoanteriorly with the descending process of the frontal in a groove and overlaps the mesial surface of the process dorsally. In older specimens it is irregularly ovoid in outline, in younger fish it is approximately rectangular.

Sphenotic. The sphenotics have a sculptured, elongate anterior portion and a broader, deeper posterior portion. The internal surface has a central trough running the length of the bone into which the frontal fits anteriorly and the pterotic posteriorly. The entire external surface is marked by rough, low ridges and depressions, the deepest of which, together with an adjacent region of the prootic, forms a facet for articulation with the hyomandibula. The lateral protuberance for the attachment of the levator arcus palatini muscle is stronger in younger fish.

Pterotic. The pterotics have a thin anterior blade enclosing a tubular channel which bears part of the postorbital canal of the lateralis system. The center of the canal is not completely enclosed by bone; either part of the canal's wall is not ossified or it is pierced by a large foramen leading to the thickened dermal tube of the third postorbital lateralis pore. Ventrally the pterotic is thickened with a strong pyramidally shaped lateral bulge. This bulge is formed by two deep internal concavities in which rest part of the semicircular canals of the inner ear. The dorsal ramus of the hyomandibula articulates in a fossa in the center of the lateral bulge.

Prootic. The prootics form the lateral and posterior margins of the trigeminofacialis foramen and the anteroventral section of the braincase. The prootic articulates dorsally with the sphenotic forming a hyomandibular condyle, the prootic portion of which lies in a low depression. The hyomandibular foramen for the passage of cranial nerve VII (nervus facialis) lies posteroventrally. The fossa for the origin of the dilator operculi muscle at the sphenotic-prootic juncture is weakly defined. The prootic is joined along most of its ventral surface by the parasphenoid, posteriorly by the basioccipital, which, together with the prootic, forms the otic bulla. The anterior portion of the sacculus lies against the mesial surface of the prootic and contains its large, discoid sagitta. Articulation with the pterotics is along the dorsoposterior surface. The internal carotid foramen is a small notch at the base of the juncture with the posterior ramus of the parasphenoid wing.

Parietal. The parietals are thin, ventrally concave, asymmetrical bones lying in the midline above the anterior process of the supraoccipital and posterior margin of the frontals. Each parietal articulates directly with its respective pterotic laterally, the posterior portion of the

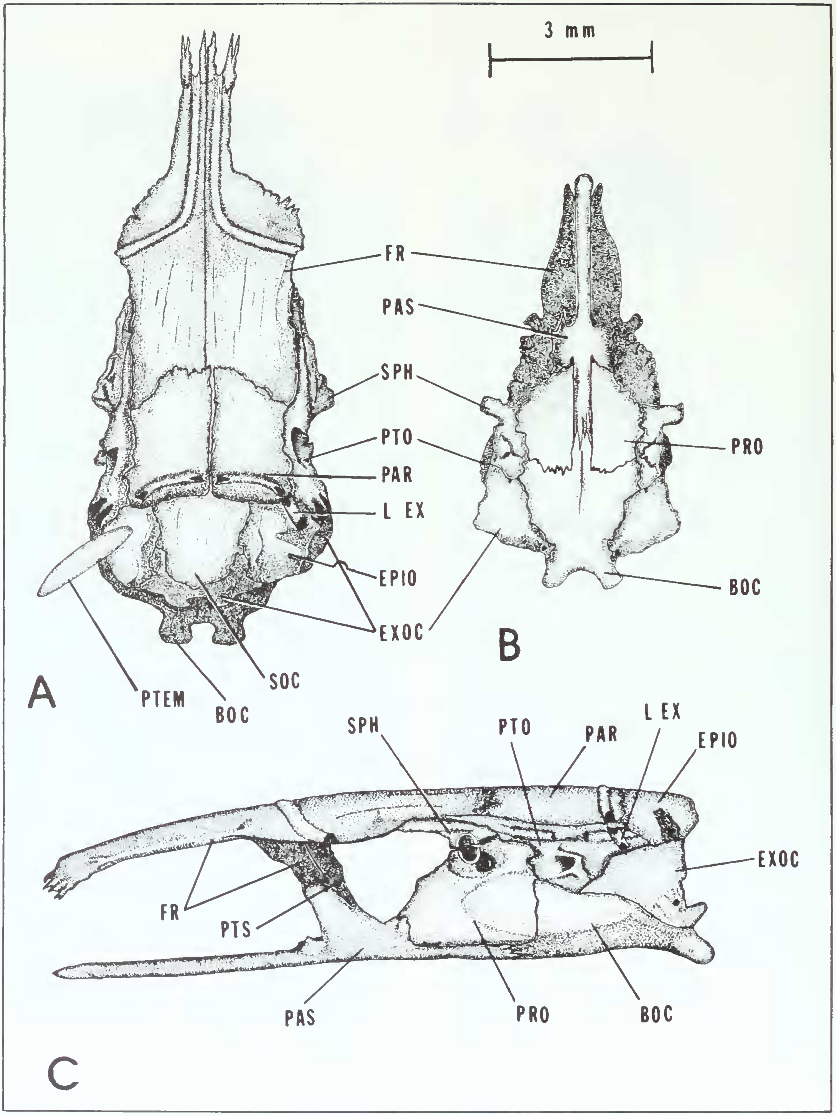

Figure 2. *Gymnelus viridis*: A) dorsal view of neurocranium of NMC 77-1259, right posttemporal and left lateral extrascapular not shown; B) ventral view of a smaller specimen of NMC 77-1259; C) lateral view of specimen in A. Ethmoid region removed in all.

supraoccipital and epioccipital posteriorly and the frontals anteriorly. The mesial edges of the parietals meet in the dorsal midline. As the bones are somewhat asymmetrical, their edges do not always parallel the exact dorsal midline of the skull. The mesial edges are very slightly farther apart in the largest specimens permitting a small portion of the supraoccipital to be viewed dorsally. Just anterior to the posterior margin, raised bony tubes, similar to those on the frontals and pterotics carry the occipital (supratemporal) canal of the lateralis system, each with lateral and mesial foramina leading to thickened dermal tubes of the lateral and mesial occipital lateralis pores.

Supraoccipital. The supraoccipital has two sections: an anterior, thin blade lying under the parietals and frontals and a broader, thickened posterior portion. The posterior portion is ventrally concave, articulating with the epioccipitals laterally and the posterior portion of the exoccipitals posteriorly. A small occipital crest is formed in fish over about 140–150 mm standard length. Only the anteriormost tip of the anterior portion contacts the frontals below. Two small lateral wings are formed about midlength; these are less pronounced in the larger specimens.

Lateral extrascapular. The lateral extrascapulars are small tubular bones suspended in connective tissue above the epioccipitals without contacting other bones. Each serves to connect the postorbital lateralis canal passing through the pterotic and the occipital canal passing through the parietals. At the posterior end a tickened dermal tube is formed for the fourth postorbital lateralis pore.

Epioccipital. The epioccipitals (epiotics) are roughly ovoid bones forming the posterodorsal edges of the skull. A shallow, irregularly shaped depression is formed on the dorsal surface for attachment of the posttemporal. This depression deepens and is more sculptured in larger specimens. Articulation is with the supraoccipital and exoccipital mesially, the exoccipital ventrally and the parietal and pterotic anteriorly. The posterior portion bulges dorsoposteriorly behind the shallow fossa where the posttemporal attaches. A low ridge for the attachment of the semispinalis longissimus muscle runs close to the mesial margin.

A low bony tube in the center of the inner surface passes the posterior vertical semicircular canal of the inner ear. In large specimens the tube becomes interrupted in the center and the canal lies against the roof of the epioccipital.

Exoccipital. The exoccipital is a large bone forming the posterolateral and part of the posterodorsal portion of the braincase. The posteroventral surface articulates with the basioccipital and forms the condyle for attachment of the first vertebra. The supraoccipital articulates along its posteromesial edge with the exoccipital, the epioccipitals dorsolaterally. It articulates with the pterotics anteriorly, and forms with them concavities separated by continuous bony laminae to house the semicircular canals. The lapillus fits in a posterior concavity of the exoccipital. The dorsoposterior edge of the sagitta lies in the anteriormost concavity. The tenth cranial nerve (nervus vagus) passes through a small foramen posteroventrally; the ninth cranial nerve (nervus glossopharyngeus) passes through a slit-like foramen anteriorly. The base of the occipital condyle is pierced with numerous foramina.

Basioccipital. The basioccipital forms the posterior portion of the otic bulla and floor of the foramen magnun. It articulates with the pterotics and exoccipital dorsally where these bones bear the horizontal and anterior vertical semicircular canals of the inner ear. Most of the posterior section of the sacculus lies in a deep concavity in the anterior portion of the bone. Articulation anteromesially is a fine interdigitation with the parasphenoid.

Jaws and Suspensorium

Figures 3, 4

Bones of the jaw and palate change shape considerably with growth in *G. viridis*. Small protuberances and depressions receiving ligaments often are reduced or accentuated in large fish.

Suborbital bones. The suborbitals are enveloped in fibrous connective tissue and form the ventrolateral border of the orbit. There are usually five, sometimes six, tubular bones with anterior and posterior foramina which are quite variably shaped in each specimen examined. The specimen illustrated, a subadult, had a relatively small third suborbital (Fig. 3). These bones pass the suborbital lateralis canal which most frequently opens in six pores. However, there is considerable variation in *G. viridis*; pores ranged from five to eleven in late juveniles and adults. The lacrymal (first suborbital) is usually the largest and possesses a foramen at its midlength opening to

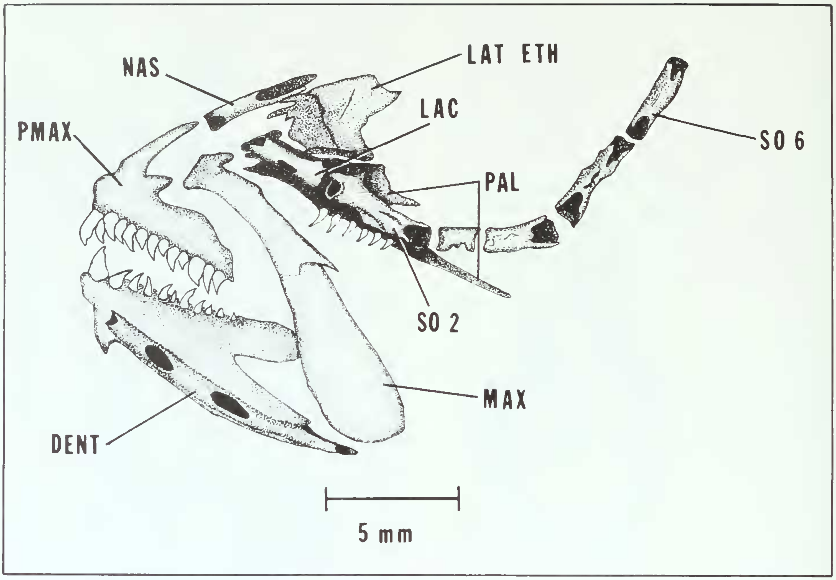

Figure 3. *Gymnelus viridis*: lateral view of suborbitals and bones associated with the jaws of NMC 62-379, anguloarticular not shown.

the second suborbital pore. Thus, the third through sixth suborbital pores (in the more typical fish) each originate from dermal tubes developed between posterior and anterior foramina in adjacent suborbital bones. All suborbitals are separate.

Premaxilla. Each premaxilla is dentigerous and has both an ascending and articulating process in small specimens which fuse in adults. Thick ligaments connect each bone along the mesial surface of the ascending process forming a movable joint. Ligaments from the maxilla insert in a shallow notch lateral to this process. Stout caniniform teeth fit in shallow depressions in a row on the ventral margin, one or two irregular rows of smaller teeth form behind these anteriorly.

Maxilla. The maxillae are edentate in Zoarcidae. They grow longer in males than females in *G. viridis*. Anteriorly the bone is subcircular in cross-section, posteriorly it is quite laterally compressed. The anterior end is thickened, roughly rounded and bears a cup-shaped depression for the attachment of ligaments joining the bone to the premaxilla. The ventral surface of the anterior end bears a low, rounded knob to which ligaments also attach joining the premaxilla. The dorsal margin of the depression forms a short dorsoposteriorly directed strut for the attachment of ligaments joining the palatine. At about the bone's midlength a small prong is usually developed on the dorsal surface. The prong is never developed in fish shorter than about 70–80 mm and occasionally is absent in adults, but in these cases the bone is thickened and is darker staining where the prong would have developed. The ligament from the A1β section of the adductor mandibularis muscle (sensu Winterbottom, 1974; levator maxillaris superioris of Rosen and Patterson, 1969) attaches around the prong. The posterior end of the maxilla is uniformly rounded and broad in specimens of all sizes. The bone rapidly tapers in the largest specimens at about the beginning of its posterior third; anteriorly it is slender and subcircular in cross section.

Palatine. The palatines lie mesial to the suborbital series and maxilla and under the lateral ethmoids. Anteriorly a broad, rounded, maxillary process attaches ligaments joining each palatine to its respective maxilla and lateral ethmoid. The anterior surface of the maxillary process has a shallow notch over which the maxilla swivels when the mouth is opened. The dorsal surface has a mesially directed, irregularly shaped wing which becomes larger and more sculptured in older fish. The ventral surface of the bone bears a row of sharp, recurved teeth. Very rarely teeth are absent in late juveniles and adults. Posteriorly a synchondrosial joint connects the palatine to the ectopterygoid.

Dentary. Each dentary bears a single outer row of moderate caniniform teeth with an inner irregular row or two of smaller teeth behind these anteriorly. It has the typical posterior V-shaped notch into which fits the anterior end of the anguloarticular. The external surface has a slightly raised, tubular ventral margin through which passes the anterior portion of the preoperculomandibular lateralis canal. This opens in three anterior, equally spaced foramina above which open the three equally spaced, anterior preoperculomandibular pores (numbers 1–3) through thickened dermal tubes. The fourth preoperculomandibular pore opens through the skin slightly posterior to the more distant fourth foramen at the posterior tip of the ventral ramus of the dentary. The anteroventral end of the bone has a moderate symphseal knob which is more pronounced in the largest specimens.

Anguloarticular. This bone is usually termed either the angular or articular but, as it is two fused bones in zoarcids, I follow Nelson (1973) in terming it anguloarticular (see also Anderson and Hubbs, 1981). The dorsal process, opposing the coronoid process of the dentary, is low and weakly defined. Dorsoposteriorly a deep, smooth, cup-shaped depression attaches ligaments from the ventral base of the quadrate which swivels above. Ventroposteriorly a low, tubular ridge passes the preoperculomandibular lateralis canal opening in anterolateral and posterolateral foramina. The fifth preoperculomandibular pore opens through a thickened dermal tube above the posterior foramen. The small, thick, L-shaped retroarticular attaches just below the posteromesial foramen. The mesial surface of the bone has a low inwardly directed ventral flange running the length of the bone. A small, triangular sesamoid articular abuts this ridge and the mesial surface of the anguloarticular. Meckel's cartilage

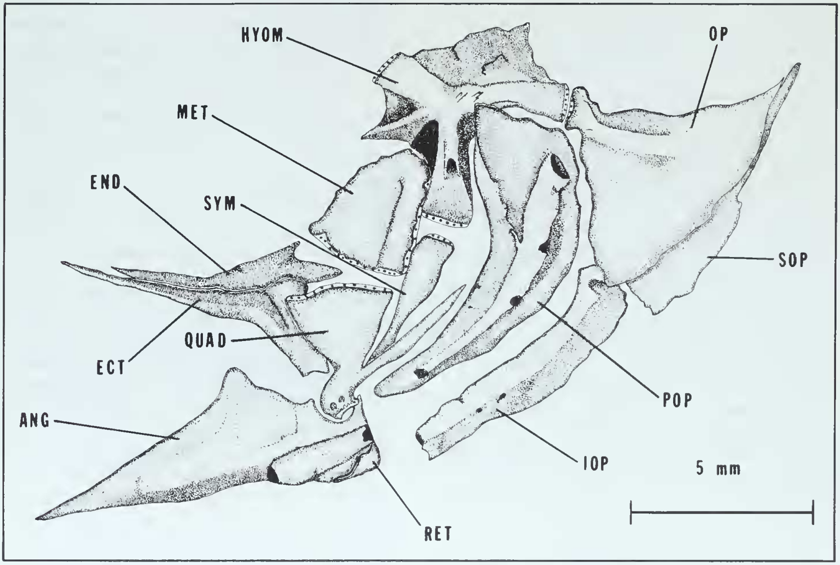

Figure 4. *Gymnelus viridis*: bones of the operculum and suspensorium of NMC 62-379.

extends across the flange and enters a bony tube posteriorly.

Ectopterygoid. The anterior, blade-like portion of each ectopterygoid is thin and flat and articulates with the posterior surface of the palatine in a synchondrosial connection that extends from the area between the quadrate and metapterygoid to the palatine head. No lateral shelf is developed. The outer surface of the posterior end is gently rounded dorsally, becoming laterally compressed ventrally. A shallow trough is formed along the posterior margin for articulation with the quadrate. A thin walled, shallow, mesial groove runs along the dorsal margin for reception of the endopterygoid.

Endopterygoid. Each endopterygoid is a dorsoventrally flattened, relatively featureless bone articulating with the ectopterygoid as described above. The posterior end has two rami which become less distinct with increasing size, between which a small notch is formed. The anteroventral tip of the metapterygoid swivels above this notch.

Metapterygoid. Each metapterygoid is a flattened, roughly triangular bone with a posterior, rounded, longitudinal ridge. The cartilaginous margin of this ridge rests in shallow troughs in the anterior margin of the lower process of the hyomandibula and symplectic. The metapterygoid is narrowly separated from the quadrate ventrally by a slight space.

Quadrate. Each quadrate has the typical dorsal, fan-shaped ramus and a strong, dorsoposteriorly directed, prong-like ramus. The ventral portion is spheroidal and swivels above the anguloarticular fossa. The anterior margin of the upper fan-like portion is thin and fits into a groove on the posterior face of the ectopterygoid. The posteroventral end of the symplectic lies in a shallow trough formed in the posterior prong.

Symplectic. Each symplectic is a thin, oar-shaped bone tapering from its broader dorsal surface to its bluntly rounded ventral tip. In larger specimens the posterior surface tends to be more sculptured than in younger fish. Also, a small flange develops on the anterodorsal margin which abuts a cartilage filled groove on the posteroventral edge of the metapterygoid. The articular surface with the quadrate has a cartilage tip which contacts the medial groove of the posterior ramus of the quadrate.

Hyomandibula. Each hyomandibula is laterally compressed and has four smoothly rounded rami, or "arms," each with a central, cartilage filled ridge. The ends of the ridges are the articular surfaces for adjacent bones and each end is convered with a cartilage pad which is continuous with the core cartilage. The dorsal arm articulates with the pterotic fossa by means of thick ligaments. The anterior arm similarly articulates with the sphenotic-prootic fossa. The posterior arm articulates with opercle and is distinctly rounded distally. The cartilage pad of the ventral arm is separated from the symplectic by means of fibrous connective tissue. A foramen for the passage of the truncus hyomandibularis nerve is present on the ventral arm. The anterior edge of the ventral arm has a narrow, thin-walled trough for articulation with the metapterygoid.

Opercular Series

Figure 4

The bones of the operculum are generally well ossified in *G. viridis*. The opercular flap is reduced and has a smooth margin due to thick sheets of connective tissues.

Opercle. The head of each opercle forms a deep, cartilage-filled, cup-shaped depression for articulation with the posterior arm of the hyomandibula. Ventral to this, on the external surface, a low, bony ridge extends posteriorly for insertion of the dilator operculi muscle. A short bony ridge develops on the internal surface of larger fish and serves to brace the opercle against the hyomandibula. The anterior end is steep and longitudinally straight to its roughly squared off corner above the dorsal end of the interopercle. The posterior margin is thin and gently sculptured, but is well ossified and without the deep finger-like indentations seen in *Melanostigma* (Yarberry, 1965) and *Derepodichthys* (Anderson and Hubbs, 1981).

Preopercle. Each preopercle is broadest dorsally and curves anteroventrally to a bluntly rounded tip. The anterior margin is generally smooth and, although thin, is rounded between the inner and outer surfaces. The posterior margin is thinner and razor-like between its inner and outer surfaces. A tubular prominence is developed on the lateral surface in young specimens for passage of the preoperculomandibular lateralis canal. This is set deeper in the bone in older fish, consequently the ridge is lower. Four foramina open in the ridge. The anteroventralmost receives the canal from the anguloarticular and does not open to a pore; the three cheek pores open from the three more dorsal foramina through dermal tubes as described previously. Two small tubes run through the bone from the preoperculomandibular canal and open on the mesial surface in two very small foramina.

Subopercle. Each subopercle is very thin but well ossified. Each lies mesial to the posterior edge of the opercle and its length is nearly contained within the dorsal and ventral edges of the opercle. At about midlength the bone is very constricted, producing a narrow, dorsal splint. The ventral end has a short anterodorsally directed strut, about as long as wide, that parallels the posterior end of the interopercle, but is separated from it by a thick mass of fibrous connective tissue.

Interopercle. Each interopercle is widest dorsoposteriorly where contact is made with connective tissue attaching the bone to the subopercle. The external surface is marked by a low ridge which is pierced by two small foramina anteriorly. The internal surface is very slightly convex. A strong flange runs from the dorsal to near the ventral edge on the mesial surface which clasps the bone to the end of the epihyal. This flange is located about at the level of the dorsal third of the bone. The ventral end slightly overlaps the ceratohyal-epihyal juncture mesially.

Hyoid Arch
Figure 5

Basihyal. The basihyal is a stout, well ossified bone, not in contact with other bones. Its posterior end lies above the ventral hypohyal. The posterior and anterior ends are laterally rounded, slightly sculptured, but the bone is generally dorsoventrally flattened. The anterior end is much broader than the posterior end.

Urohyal. The relatively large urohyal is connected to the floor of the branchial basket by means of thick sheets of connective tissue. It is strongly laterally compressed with a relatively straight anterior edge and a highly sculptured posterior margin. The sternohyoideus muscle inserts on the lateral surfaces.

Hypohyal. There are two paired ossifications of the hypohyal in *G. viridis*. The dorsal hypohyal is a shell of cartilage-filled bone which articulates in an anterior groove of the ceratohyal into which passes the central cartilage mass. The lateral and mesial surfaces interdigitate with the respective surfaces of the ceratohyal. Ventrally the dorsal ossification articulates with the ventral hypohyal. The ventral hypohyal has a similar central cartilage mass and interdigitates with the ceratohyal on its lateral surface. The ventral surfaces of the ventral hypohyal is prolonged into a posteriorly directed ramus which lies on the

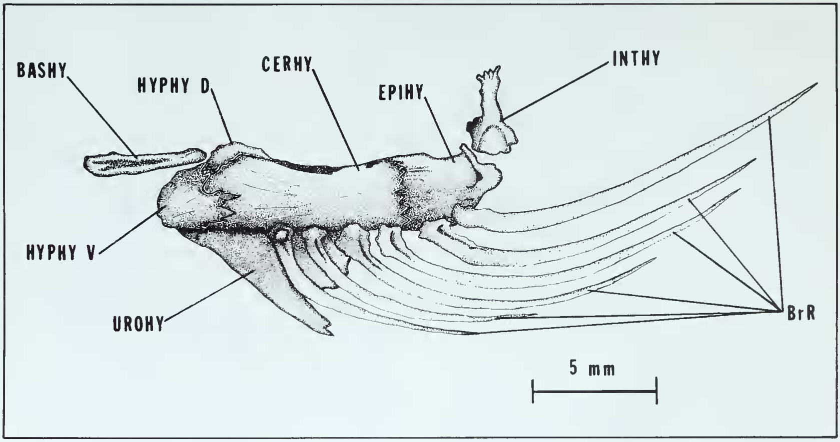

Figure 5. *Gymnelus viridis*: lateral view of bones of the left hyoid arch of NMC 77-1259.

floor of the anterior groove of the ceratohyal.

Ceratohyal. The central portion of each ceratohyal is slightly dorsoventrally constricted and thinner than the two ends. The inner surface is flattened, the outer gently rounded. A deep anterior groove is cut into the bone for reception of the hypohyals as described above. The dorsal hypohyal forms the roof of this groove but the floor is formed by the ceratohyal, along which rests the posterior branch of the ventral hypohyal. Four branchiostegal rays insert on the ventral surface, very rarely five or three.

Epihyal. Each epihyal is a roughly triangular bone interdigitating with the posterior end of the ceratohyal. Like the ceratohyal it is mesially flattened and laterally more rounded. The posterior end is sculptured producing a rounded knob above which the interhyal swivels. Two branchiostegal rays insert on the ventral surface in all specimens examined.

Interhyal. Each interhyal is an irregularly shaped bone which is separated from the epihyal by thick fibrous connective tissue. A deep cup-shaped fossa is present on the ventral and where the bone swivels above the epihyal. The dorsal end is sculptured where thick ligaments attach the bone to the symplectic-hyomandibular interspace.

Branchial Basket

Figure 6

The bones of the branchial basket are generally tubular or barrel-shaped. The basket is held together and suspended from the skull and hyoid arch by means of thick sheets of connective tissue. Several elements found in more primitive teleosts have been fused or lost in *G. viridis*.

Basibranchials. The first three basibranchials are ossified in *G. viridis* and lie in the midline; the

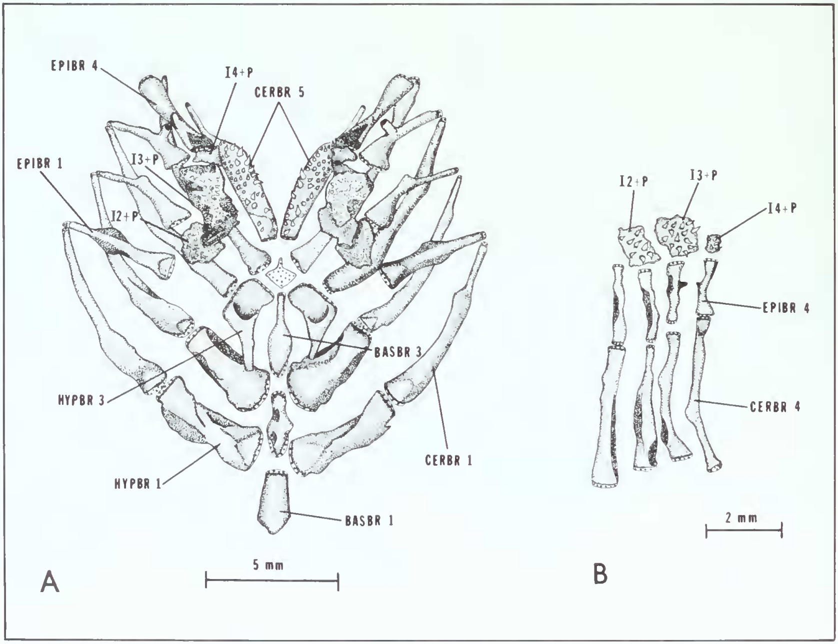

Figure 6. *Gymnelus viridis*: A) dorsal view of branchial basket of NMC 77-1259; B) ventral view of upper gill arch bones and tooth plates of another specimen of NMC 77-1259, epibranchials and tooth plates stretched to lie in same plane as ceratobranchials.

fourth is a roughly diamond shaped mass of cartilage. Each is dorsoventrally rounded but the first is flatter and more smooth-edged, especially in larger fish. The second and third basibranchials have central constrictions and sculptured sides.

Hypobranchials. There are three pairs of ossified hypobranchials. The first two are relatively larger, more tubular and with more sculptured sides than the third. The first and second hypobranchials have low, lateral wings for attachment of the obliqui ventrales muscles. The third hypobranchials are roughly fan-shaped with a rod-like anteriorly directed portion and a flattened posterior section. The obliquus ventralis muscle of the third gill arch attaches to the ventral surface of the third hypobranchial but no sculptured ridge or prominence is present. The dorsal surface of the third hypobranchial has a shallow fossa into which the third ceratobranchial fits when the branchial basket is depressed.

Ceratobranchials. There are five pairs of roughly oar-shaped, well ossified ceratobranchials. The first through third have thicker anterior ends than posterior ends for attachment of each respective obliquus ventralis muscle connecting the ceratobranchials and hypobranchials. The fourth ceratobranchial is the longest bone of the branchial basket and is more tubular than other bones. The fifth ceratobranchial is thickened and dorsoventrally flattened. It bears about 25–30 small, upwardly directed, acrodont teeth.

Epibranchials. There are four pairs of edentate epibranchials. The first are subcircular in cross-section anteriorly with thin, lateral wings posteriorly and are ligamentously suspended from the base of the neurocranium. The second through fourth epibranchials are more laterally compressed than the first. The second and third epibranchials are thicker and broader anteriorly than posteriorly; the fourth epibranchial has approximately equally thick anterior and posterior ends with a strong central constriction. The third and fourth epibranchials have well developed, upwardly directed uncinate processes; the uncinate process of the second epibranchial is weakly defined, especially in small specimens.

Infrapharyngobranchials. There are three pairs of infrapharyngobranchials, each with a fused tooth plate on its ventral surface. The pairs correspond to gill arches 2–4, the first infrapharyngobranchial has been lost in zoarcids (Anderson and Hubbs, 1981). The second epibranchial is directly posteroventral to the second infrapharyngobranchial and its fused tooth plate, but part of the anterior tip of the first epibranchial rests above the dorsal surface of the second infrapharyngobranchial when the branchial basket is depressed. The third infrapharyngobranchial and its tooth plate is the largest upper pharyngeal element; it is roughly rectangular, but there is significant individual variation in the shapes of these bones. The fourth infrapharyngobranchial, the smallest of the three, fits in a fossa on the anterior end of the epibranchial when the branchial basket is depressed.

Pectoral Girdle

Figure 7

The structural details of the pectoral girdle are similar to those of *Melanostigma*, another zoarcid without pelvic fins (Yarberry, 1965) and *Neozoarces* (Makushok, 1961). Unlike *Melanostigma*, *G. viridis* has four actinosts and unlike both *Neozoarces* and *Melanostigma* there is a slight ventral fork on the posttemporal. The pectoral girdle of *G. viridis* bears little resemblance to that of *Derepodichthys* (Anderson and Hubbs, 1981). Thick sheets of connective tissue surround all the bones and bind the cartilaginous bases of the pectoral fin rays to the cartilaginous posterior rim surrounding the actinosts and scapula.

Posttemporal. Each slender posttemporal articulates with the skull in a depression on the epioccipital as described above (Fig. 2). The anterior articular surface is dorsoventrally flattened. Posterior to this the bone is slightly curved and has a short ventral fork.

Supracleithrum. Each supracleithrum has a deep cup-shaped depression dorsally above which swivels the posterior end of the posttemporal. A lateral ridge runs from the dorsal end to about midlength. The ventral third is more laterally compressed than the remainder since the lateral ridge is not present.

Cleithrum. Each cleithrum has a deep, dorsal, T-shaped fossa on its lateral surface above the horizontal axis of which swivels the supracleithrum. Dorsoposteriad to this is the incompletely ossified dorsal lamina, which is slightly better ossified in *G. viridis* than *Melanostigma* (Yarberry, 1965) or *Derepodichthys* (Anderson and Hubbs, 1981). Along the mesial surface an anterior ridge is formed, posterior to which is a long, deep fossa (cleithral trough) for the

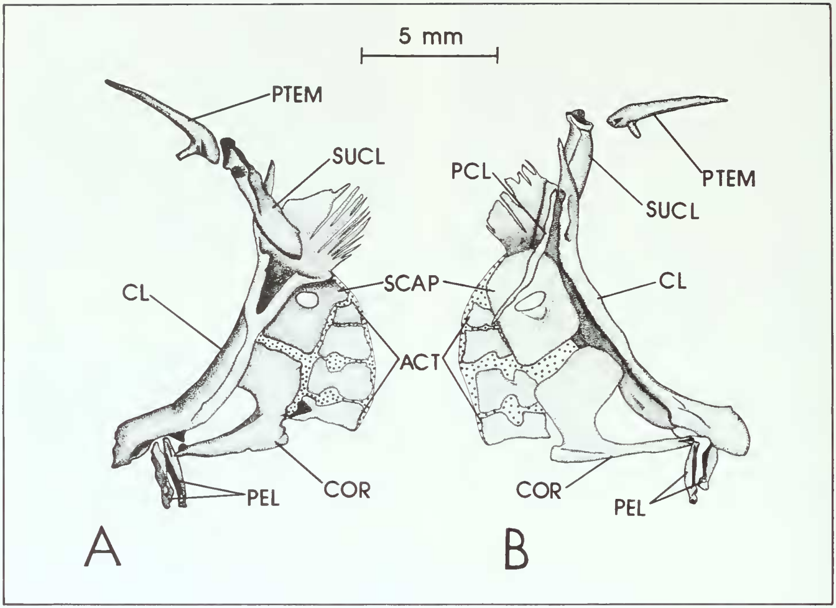

Figure 7. *Gymnelus viridis*: A) lateral view of bones of the pectoral girdle of NMC 77-1259; B) mesial view of same of NMC 62-410. Posttemporals pulled dorsally and posterior ends of pelvic bones placed ventrally to *in vivo* positions in both.

attachment of the pectoral fin adductor muscles. The anteroventral end has a shallow fossa into which runs a ligament attaching the pelvic bones to the cleithrum. Posterior to this, on the mesial surface, is a small triangular, ventrally directed strut which abuts a similar dorsally directed strut on the coracoid. The paired cleithra are ligamentously attached at their anteroventral ends. From this region the sternohyoideus muscle originates, inserting on the urohyal anteriorly.

Postcleithrum. Each postcleithrum is needle-like, slightly bowed and is not in contact with other bones, being suspended in the thick sheets of connective tissue that surround the pectoral girdle. Each extends from about the dorsal edge of the dorsal lamina of the cleithrum to opposite the second or third actinost. The postcleithra are mesial to all other bones of the pectoral girdle. They are relatively longer in older fish.

Scapula. Each scapula is a thin, roughly rectangular bone occasionally with anterior and posterior dorsal expansions (Fig. 7A). The scapulae are generally featureless except for these expansions which are about as often absent as present, independent of size. The scapular foramen is completely enclosed by bone.

Coracoid. The coracoids attain a variety of shapes in *G. viridis* apparently correlated with the size of the fish. Each is composed of two main sections: a laterally compressed dorsal part which, like the anterior margin of the scapula, attaches to the mesial cleithral trough by means of connective tissue, and a ventral rod-like portion which attaches to the ventral strut of the mesial surface of the cleithrum. The postero-mesial surface is smooth ventrally; at the juncture of the lower rod-like section a low ridge is present to which the coracoradialis muscle is attached. Occasionally a small foramen pierces the dorsoposterior portion of the dorsal part of the bone.

Actinosts. There are four separate actinosts, the dorsal two of which are the smallest and are roughly rectangular, the ventral two roughly hour glass-shaped. The bones are quite laterally compressed, yet the edges are well ossified. Ten to 14 pectoral fin rays attach to a thin cartilaginous rim along the posterior margins of the actinosts or, dorsally, to the dorsoposterior edge of the scapula. This cartilage is continuous with that separating the actinosts and scapula and coracoid.

Pelvic bones. Pelvic fin rays are absent in *Gymnelus*; no trace of rudimentary rays was ever found. Each pelvic bone is attached by a ligament to a shallow fossa on the cleithrum. The *in vivo* position of the bones is with the longest axis pointed cephalad-caudad; their position in Figure 7 is for clarity. The posterior tips contact each other mesial to about half the length of the ventral rod-like portion of the coracoid.

Axial skeleton

Figures 8, 9

The axial skeleton consists of the vertebral column, ribs and pterygiophores of the unpaired fins and the caudal skeleton. There is considerable individual variation in the number and positions of many of these elements.

Vertebrae. The vertebral centra are amphicoelus and asymmetrical (central constriction shifted anteriorly). They usually bear low lateral ridges and are infrequently pierced with foramina. The first two vertebrae are strongly anteroposteriorly compressed. Neural arches are complete on all vertebrae, are highly sculptured and usually are pierced with one or two lateral foramina. The first complete haemal arch appears on vertebrae 19–24, thus there are 18–23 precaudal vertebrae. The neural pre- and postzygapophyses are developed into long, dorsally directed prongs away from the origin and insertion of the dorsal fin. The haemal pre- and postzygapophyses are weak on most precaudal vertebrae, becoming well defined sharp struts on the caudal vertebrae. The caudal vertebrae are larger and more anteroposteriorly compressed than most of the precaudal vertebrae.

Ribs. The pleural ribs articulate with vertebrae anteriorly and are thick and slightly posteriorly curved. Posteriorly they become short and slender and usually have thinly ossified tips causing a twisted appearance. These ribs are inserted from the midlateral surface of the second or third vertebra and posteriorly assume an increasingly more ventrolateral position. They extend to off the penultimate precaudal vertebra, where they "float" in the epaxial myomeres. The epipleural ribs are long, recurved and needle-like anteriorly, becoming small splints posteriorly. They extend from the second to tenth or eleventh vertebra.

Dorsal fin. The dorsal and anal fins in *G. viridis* are long and low, extending completely along the tail and are confluent with the caudal fin. The proximalmost pterygiophores appear to be a fusion of the proximal and median elements and are termed here, simply, proximal pterygiophores. These pterygiophores, as well as those of the anal fin, are said to be associated with the vertebra with its neural (or haemal) spine directly anterior to it. One dorsal fin proximal pterygiophore is associated with the second or third vertebra and one each for all remaining vertebrae minus the fourth or fifth preural vertebra. Figure 8 shows an anomalous fusion of the first two proximal pterygiophores and the association of the first dorsal fin element (a hard spine; see below) with the third pterygiophore. This condition was not noticed in any other specimen examined by x-ray or alizarin preparation (some 190 fish). The usual condition is for the first dorsal spine to be associated with the first or second (very rarely the third) unfused proximal pterygiophore. Distal pterygiophores are present as small cartilaginous spheres located at the base of every dorsal fin ray.

The first dorsal fin ray is a hard spine; it is short, stiff, not bilaterally divided and is without segmentation or distal branching. It often has highly irregular lateral edges when viewed either anteriorly or posteriorly. Posteriorly, for a variable distance, the fin rays are the so-called "flexible spines" which, although stiff and distally unbranched, are bilaterally divided at least near their bases and are segmented. Rays toward the middle of the fin are divided for nearly half their length. The last dorsal fin ray is associated variably with the fourth or fifth preural vertebra.

Anal fin. All anal fin rays are true soft rays (bilaterally divided, segmented). The first anal ray is most frequently unbranched distally. Between one and three proximal pterygiophores are inserted anterior to the haemal spine of the first caudal vertebra, posteriorly each pterygiophore is associated with one vertebra, as in the dorsal fin, except for an anomalous few with two pterygiophores between the haemal spines of the first and second or second and third caudal

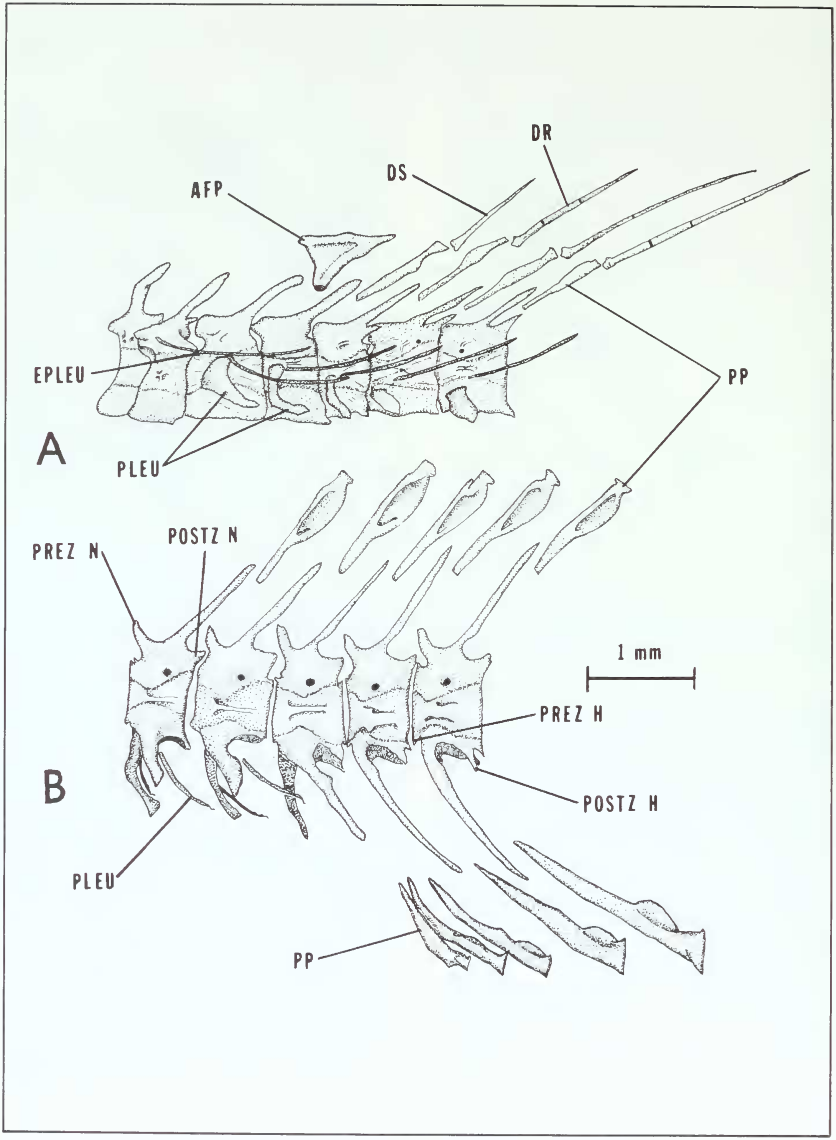

Figure 8. *Gymnelus viridis*: A) first seven vertebrae of NMC 62-410 with anomalous fused first and second pterygiophores; B) vertebrae 18-22 of same specimen, fin rays not shown.

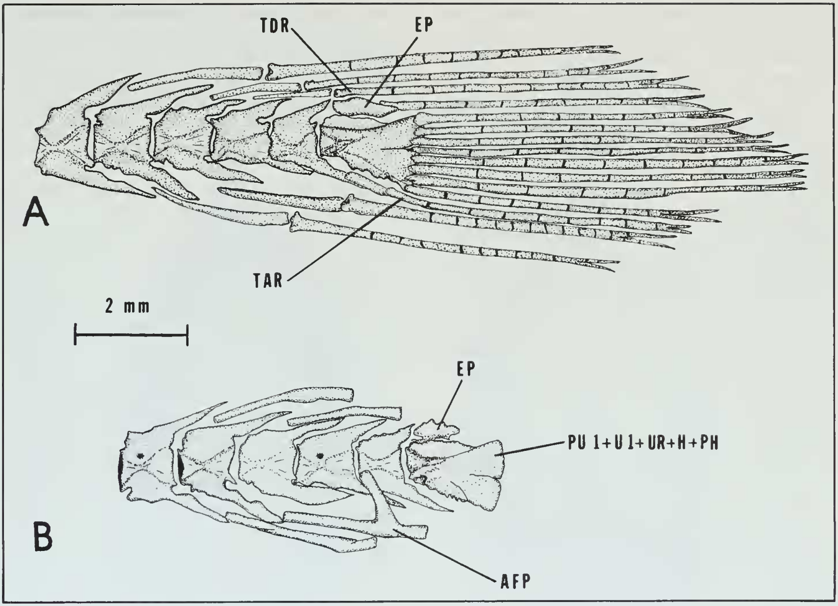

Figure 9. *Gymnelus viridis*: A) caudal skeleton of NMC 77-1259; B) same of another specimen of NMC 77-1259 showing anomalous fused pterygiophores associated with preural vertebrae 4-5; fin rays not shown.

vertebrae. The last anal fin ray is associated invariably with the second preural centrum and there is no distal pterygiophore. The proximal pterygiophore of this vertebra is greatly reduced and joined with the haemal spine, thus the fin ray appears to be attached to the spine. Figure 9B shows an anomalous fusion of the pterygiophores of the fourth and fifth preural vertebrae—this element bore only one ray and this condition was observed in six fish.

Caudal skeleton. The rays of the caudal fin articulate with the single epural and fused hypural plate. There are one to three rays associated with the epural (these may be directly attached or "float" in connective tissue behind) and seven to nine rays attached to the hypurals. There are no distal pterygiophores. The first preural and ural centra, uroneural, parhypural and hypurals (probably hypurals 1–4, see Anderson and Hubbs, 1981, Fig. 10) are fused. Occasionally part of the single epural fuses with the uroneural.

Comparative Remarks

A small group of western North Pacific species appears most closely related to *Gymnelus* and *Gymnelopsis* based on the general architecture of the neurocranium and ethmoid region, opercular apparatus, axial skeleton, lateralis canals and pore distribution, meristics and their small size. These species are currently placed in the genera *Krusensterniella*, *Davidijordania*,* *Bilabria*, *Hadropareia* and *Lycozoarces*, which were placed in various subfamilies by Shmidt (1950) and Lindberg (1971, 1974). DeWitt (1977) referred his new genus, *Exechodontes*, from the Gulf of Mexico, to Shmidt's (op. cit.) Hadropareinae, which included *Davidijordania*, *Bilabria* and *Hadropareia*. Shmidt (op. cit.) placed *Krusensterniella* and *Lycozoarces* in subfamilies Zoarcinae and Lycozoarcinae respectively. These decisions

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*Shmidt (1936) improperly emended *Davidijordania* Popov to *Davidojordania*, a fact first noted by DeWitt (1977).

were seemingly based on few characters; no diagnoses were given. DeWitt (op. cit.) gleaned a diagnosis of Hadropareinae mostly from Lindberg and Krasyukova's (1975) key.

A thorough phylogenetic analysis to test hypotheses of relationships is beyond the scope of this paper and pending future comparative study, I tentatively refer all the above genera, except *Exechodontes*, to subfamily Gymnelinae Gill, 1864. The relationships of *Exechodontes* are presently unclear, but it seems close to the Gymnelinae. However, this preliminary study has not resolved monophyletic groups satisfactorily at any level and the tentative Gymnelinae may also include *Zoarces* (Anderson, unpubl. data).

The following comparisons of the morphology of *Gymnelus* and *Gymnelopsis* species are based on cleared and stained bone preparations of all *Gymnelus* species, except *G. pauciporus*, and of *Gymnelopsis ochotensis*, *Davidijordania poecilimon* and *Lycozoarces regani*. Radiographs and superficial dissection of other genera aided the study, and these are listed in Appendix II.

Neurocranium and ethmoid region. The ethmoid region of all species of *Gymnelus* is similar to that of *G. viridis*. A strong lateral ridge is formed in *Gymnelopsis ochotensis* on each side of the mesethmoid to which attach the ligaments from the maxilla and palatines; this is weakly defined in all *Gymnelus*. The mesethmoid does not contact the vomer and parasphenoid in all gymnelines examined.

In the largest adults examined (*Gymnelus viridis*, 215 mm SL, *Gymnelopsis ochotensis*, 252 and 222 mm SL, *Lycozoarces regani*, 152 mm SL), the frontal bones bowed upwardly in the region of mid-orbit (Fig. 10). In young fish, presumably including *Gymnelopsis* and *Lycozoarces* species, they are relatively straight in lateral view. Posterior to the area of the bow, in *G. popovi* and all *Gymnelopsis*, an elongate foramen is present in the tube in the frontals passing the supraorbital canal. This foramen leads to a tube of connective tissue opening through the skin as the interorbital pore. The foramen is set more posteriorly in *Gymnelopsis ochotensis* and *Lycozoarces regani* than in *G. popovi*, as is the interorbital pore, but the pore is about at the same level relative to the eyes in *G. popovi*, *Gymnelopsis brevifenestratus* and *G. ocellatus*.

The anterior ramus of the parasphenoid wing extends upwardly to half the height of the trigeminofacialis foramen in all *Gymnelus*. It is higher and broader in *Gymnelopsis ochotensis*, *Lycozoarces regani* and *Davidijordania poecilimon*, extending upwardly to about 80% of the height of the foramen. In these species with more dorsoventrally flattened skulls than *Gymnelus*, the descending wings of the frontals and the pterosphenoids are larger, thicker and more sculptured.

The tubular channel passing the occipital (supratemporal) lateralis canal across the parietals is similar in all gymnelines examined except for *Gymnelus hemifasciatus* and *G. retrodorsalis*. The canal passes along a low, irregular bony shelf at the posterior edge of the parietals in these latter species and is continuous across the nape. Stain injection of the canal revealing this continuity was successful only in recently preserved specimens. Half of the partially ossified bony parietal tube is continued over the pterotics in *G. retrodorsalis*, the other half extends mesially across the parietals to half its width. Most *G. hemifasciatus* and *G. retrodorsalis* possess only two occipital pores and the bony shelf is continued farther, opening in another foramen, as in *G. viridis*, in those fish with three occipital pores. From these observations it seems most likely that the bony parietal tube and canal are not developed in gymnelines without occipital pores. The lateral extrascapulars are displaced to a position over the posteriormost section of the pterotics in adult *G. retrodorsalis*, instead of over the epioccipitals, as in the species noted above. There are two pairs of lateral extrascapulars in *Lycozoarces regani*, one over, one posterior to the pterotics, connecting the occipital and postorbital canals, unlike the one pair in other gymnelines examined. The mesial edges of the parietals are laterally displaced farther from the dorsal midline of the skull in adult *Gymnelopsis ochotensis* (Fig. 10), *D. poecilimon* and *L. regani* than in *G. viridis*.

The supraoccipitals of all species examined are roughly similar in shape; with age the lateral wings of the posterior portion become less distinct, while the occipital crest becomes more distinct. The anterior supraoccipital blade is greatly extended in *G. popovi* and anteriorly extends under the frontals beyond the anterior edge of the sphenotics (Fig. 11).

No significant differences in structure or articulation were found among other neurocranium bones of the species examined. Radiographs of *Hadropareia*, *Lycozoarces*, *Bilabria* and *Krusensterniella* revealed gross overall

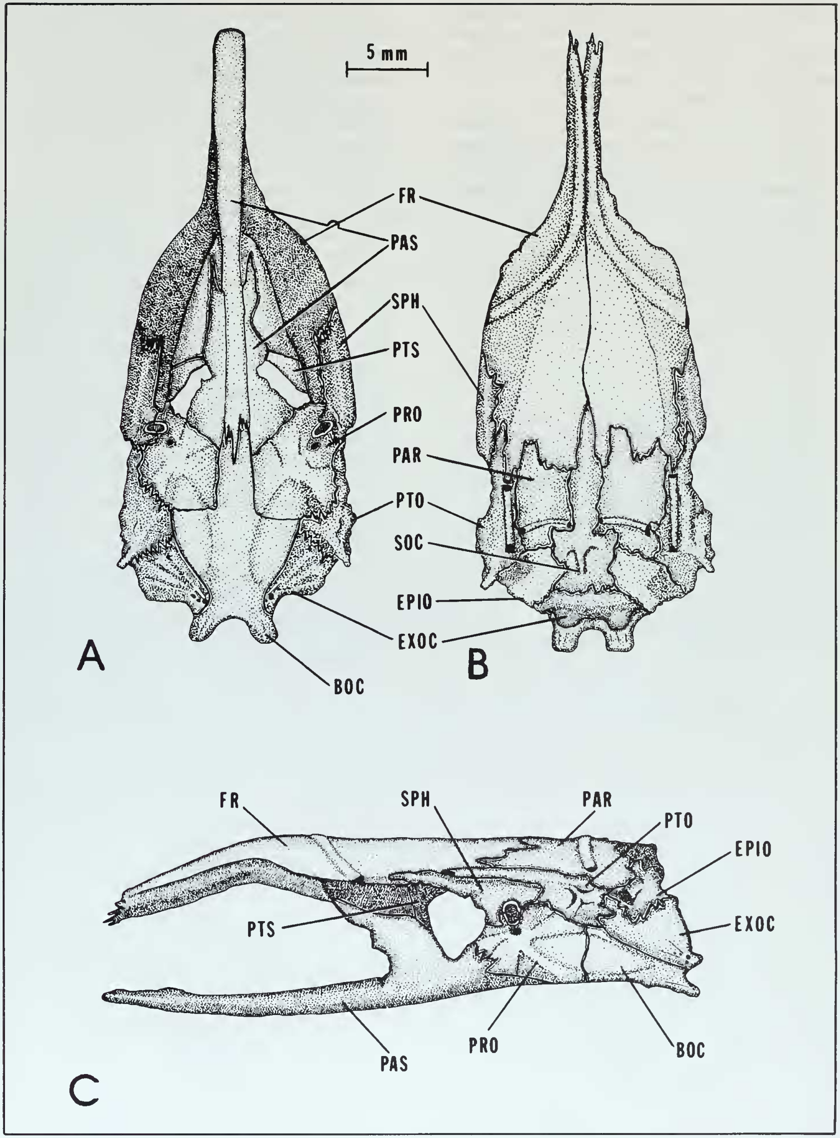

Figure 10. Neurocranium of *Gymnelopsis ochotensis*, UMMZ 202550. A) ventral, B) dorsal and C) lateral views. Ethmoid region and lateral extrascapulars removed in all.

similarities, but these were generally inadequate for detailed observation. Due to inadequate sample sizes, no attempt was made to discern patterns of similarity among the sagittae of the gymnelines studied.

Jaws and suspensorium. The number of preoperculomandibular pores and their relation to foramina in bones of the lower jaw and cheek is characteristic of species groups in gymneline eelpouts. No observations are available on *Hadropareia*.

All species of *Gymnelus*, except *G. pauciporus*, have four dentary preoperculomandibular pores; these emerge from three closely spaced anterior and one posterior foramina (the latter exits at the tip of the ventral ramus, Fig. 3). In *G. pauciporus* pores number one and three (numbered anterior to posterior) are absent (Fig. 12). In *Gymnelopsis* only three foramina develop normally leading to pores number one, two and four (Fig. 13). In *G. ochotensis*, however, only pores one and four or two and four develop (Fig. 14). This reduced state is also seen in *Krusensterniella*; the pattern in *Davidijordania*, *Lycozoarces* and *Bilabria* is usually identical to that of *Gymnelus*. Toyoshima (1981) reports this similar condition in *L. regani*, yet the two specimens I observed lacked dentary pore 3. One was cleared and stained and no foramen for pore 3 was developed.

All gymnelines have one foramen exiting to the fifth preoperculomandibular pore (in the complete system, i.e., *Gymnelus* and others) at the posterior edge of the anguloarticular. The coronoid process of the anguloarticular in *G. ochotensis* and *L. regani* is greatly reduced compared to *Gymnelus*, but this is partly a growth characteristic (Fig. 13).

Four foramina open in the preopercular tube passing the preoperculomandibular canal up the cheek in all *Gymnelus* except *G. pauciporus*. The dorsalmost three lead to the cheek pores (Fig. 4). Only the central and dorsal preopercular pores are present in *G. pauciporus*, presumably only the upper two preopercular foramina are present, plus the ventralmost, which never leads to a pore in gymnelines. The two ventralmost foramina in the preopercle leading to pores are set slightly lower in *Gymnelopsis ochotensis* and *Davidijordania poecilimon* than *G. viridis*. This is presumably the case in other *Gymnelopsis* species, which all have three preopercular foramina leading to pores, except *G. brevifenestratus* which has two. Unlike *Gymnelus pauciporus*, however, the ventral and dorsal foramina leading to pores are present in *G. brevifenestratus*, not the central and dorsal. Three almost evenly spaced preopercular pores are also present in *Bilabria*, *Kursensterniella* and *Lycozoarces*.

The vomer, palatines, dentary and premaxillae

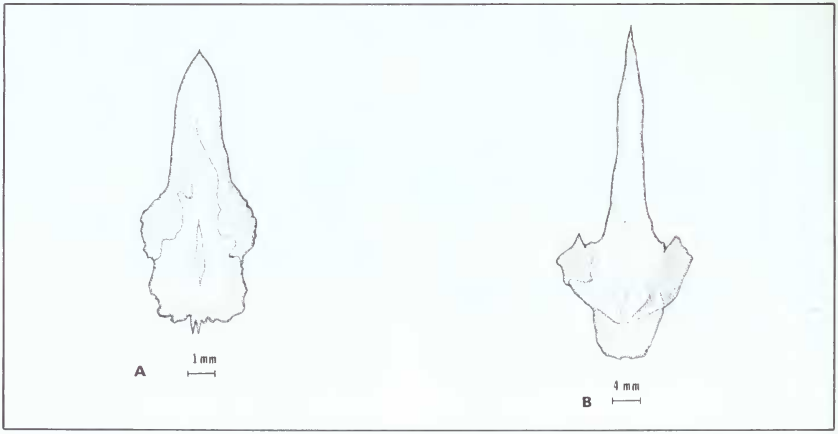

Figure 11. Dorsal view of supraoccipitals of A) *Gymnelus viridis*, ZMUC 8 and B) *Gymnelus popovi*, UWZ 3558.

REVISION OF THE FISH GENERA *GYMNELUS* REINHARDT AND *GYMNELOPSIS* SOLDATOV (ZOARCIDAE), WITH TWO NEW SPECIES AND COMPARATIVE OSTEOLOGY OF *GYMNELUS VIRIDIS*

bear generally larger, more numerous teeth in *Gymnelopsis*, *Davidijordania*, *Lycozoarces* and *Bilabria* species than in equally sized *Gymnelus* or *Krusensterniella* species (palatine teeth absent in *Bilabria ornata*). The maxillae grow slightly longer in males than females in all gymneline eelpouts. The vomer and the palatines of *Gymnelus popovi* are edentate; the ventral surfaces of these bones are smooth and no trace of tooth sockets is found. This is the sole unique character (autapomorphy) of this species and is insignificant by itself to establish a genus separate from *Gymnelus*. Other characters that distinguish this species (presence of the interorbital pore, the far forward dorsal fin origin) are considered primitive within the species group, and are not used at the generic level. Additionally, some characters given by Taranets and Andriashev (1935) and Andriashev (1937) to establish a separate genus (*Commandorella*) for this species simply do not exist (reduced lateral line, structure of lower lip and pectoral fin).

There are no significant differences in the structure or articulation of the remaining suspensorium and jaw bones of other gymneline eelpouts with those of *G. viridis*.

Only minor structural differences of no significance exist among the bones of the opercular region in all gymnelines under consideration except for those of the preopercles noted above.

Hyoid arch and branchial basket. The structure and articulation of all the bones of the hyoid arch and branchial regions are quite similar in all gymnelines—similar to the conditions in most zoarcids (Anderson and Hubbs, 1981). Six branchiostegal rays are usually found in *Gymnelus*, with *G. hemifasciatus* (and the limited known material of *G. pauciporus*) having the highest percentage of aberrant individuals (see these species' accounts below). Five branchiostegal rays are present in *Gymnelopsis*, except in *G. ocellatus*, which has six (as far as known). *Krusensterniella* also possesses five branchiostegal rays with articulation as in *Gymnelopsis* (Fig. 15). *Davidijordania*, *Bilabria* and *Lycozoarces* possess six rays and *Hadropareia* seven or eight.

All gymneline eelpouts have four gill arches

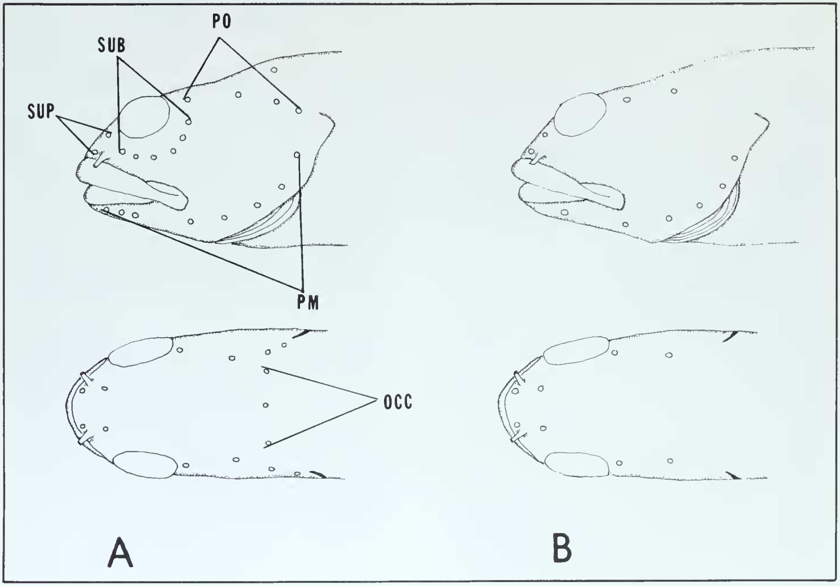

Figure 12. Typical head pore patterns of A) *Gymnelus viridis* and B) *Gymnelus pauciporus* n. sp.

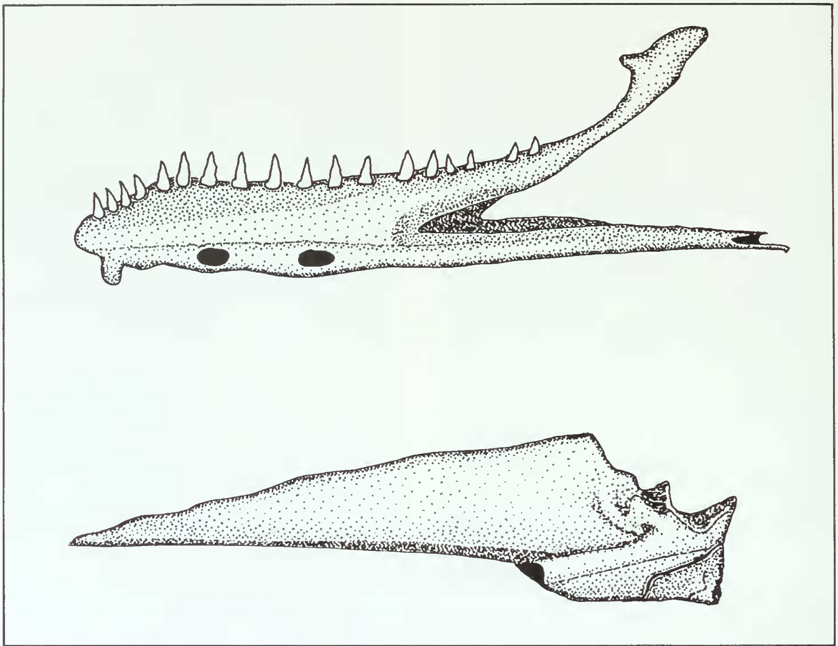

Figure 13. Bones of the lower jaw of *Gymnelopsis ochotensis*, UMMZ 202550; upper, dentary, lower, anguloarticular.

with a slit behind the fourth occupying half the height of the arch, three infrapharyngobranchials and fused tooth plates, toothed fifth ceratobranchials and three ossified basibranchials, all as in *G. viridis* (Fig. 6).

Pectoral girdle. Very few differences in the structure of the pectoral girdle exist in gymneline eelpouts. The shallow dwelling species (*Gymnelus viridis*, *G. popovi*) have longer ventral processes of the posttemporal than the deeper living forms (especially *G. retrodorsalis* and *G. hemifasciatus*, the latter has no ventral process). The dorsal lamina of the cleithrum is more reduced in the deeper dwelling species; either the laminar surface is smaller in size, or equal in size but less ossified, than in *Gymnelus viridis*.

Few other differences exist among the pectoral girdle bones in all gymnelines; four actinosts are present in all species. The coracoid and scapula of *Gymnelopsis ochotensis* have a short posterior directed flange on the posteroventral edges of the bones for muscle attachment. The pelvic bones are reduced to paired, ovoid or splint-like ossifications in *Gymnelus*, *Gymnelopsis* and *Krusensterniella* (all without pelvic fins); they are larger and more dorsoventrally flattened in the genera with pelvic fins (*Davidijordania*, *Bilabria*, *Lycozoarces* and *Hadropareia*). There are three rays in each pelvic fin in these latter genera.

Axial skeleton. The vertebrae are amphicoelus and asymmetrical in all gymnelines. Pleural ribs are present from vertebrae 2–3 to the antepenultimate or ultimate precaudal vertebra in all, depending on species. Epipleurals extend from the first or second vertebra to the central region of the precaudals (usually vertebrae 10–15; on vertebrae 1–7 in *Gymnelus retrodorsalis*), depending on the species or individual.

A few species of *Gymnelus* and *Gymnelopsis* often have no dorsal fin rays associated with the first few pterygiophores—the number is

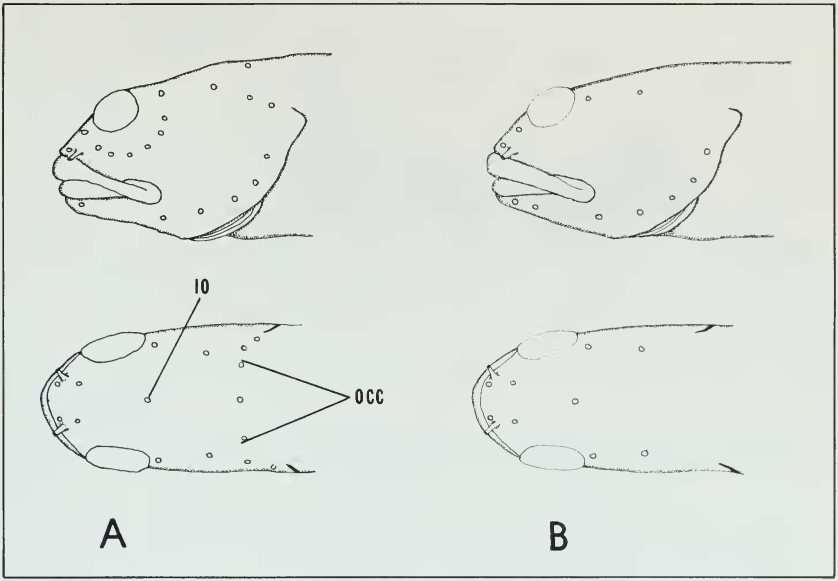

Figure 14. Typical head pore pattern of A) *Gymnelopsis ochotensis* and B) *Gymnelopsis ocellatus*. Compare with Figure 12.

individually variable (discussed below). The first dorsal fin ray is a hard spine, the remaining are soft rays in all *Gymnelus* and *Gymnelopsis* examined. *Lycozoarces* has two anterior dorsal fin spines. The first two dorsal fin rays (a spine and a soft ray) of *G. popovi* and their pterygiophores are often situated between the neural spines of the first and second vertebrae; the pterygiophores are often fused in this condition. Rarely is the first dorsal pterygiophore of *G. popovi* without its associated spine. About the first 2/3 of the dorsal rays are hard spines in *Krusensterniella*, including the few stout, pungent spines that are characteristic of this genus (Andriashev, 1938; Makushok, 1961; pers. observ.). The first dorsal ray in the one specimen of *Davidijordania poecilimon* examined was bilaterally divided along its length, but not branched or segmented. As this was a juvenile it appears that the character had not reached full expression. The character was not observed in *Bilabria* or *Hadropareia.*

The caudal skeletons of gymneline eelpouts exhibit some interesting differences. The hypurals and parhypural are fused to each other along their length and the urostyle in all genera except *Lycozoarces*, which has a separate upper and lower hypural, and fused only at their anterior ends. The two hypural elements correspond to hypurals 1–2 (lower) and 3–4 (upper) (Anderson and Hubbs, 1981). *Lycozoarces* also possesses one epural not fused to the uroneural with two or three associated fin rays; all other genera possess an epural fused to the uroneural with one to three associated fin rays. Three groups of genera are separable by the number of caudal fin rays: 1) *Hadropareia* (with 7–8 rays), *Gymnelopsis* and *Krusensterniella* (5–7 or 8); 2) *Gymnelus* and *Davidijordania* (9–10 or 12); and 3) *Lycozoarces* (13–15). Three groups are also separable by the total number of vertebrae, one with low counts, an intermediate and one with high counts: 1) *Lycozoarces* (65–71); 2) *Gymnelus* (85–105); and 3) *Gymnelopsis* [106–114, except *G. brevifenestratus* (89–96)], *Krusensterniella* (109–119), *Davidijordania* (100–119), *Bilabria* (118–119) and *Hadropareia* (110–114).

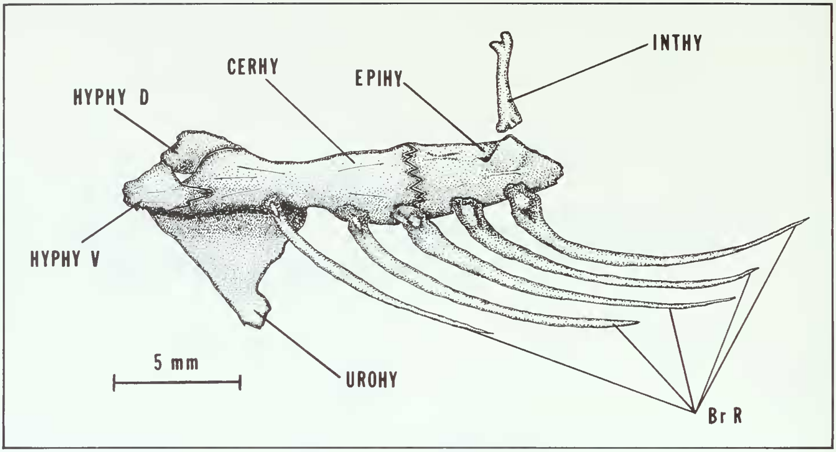

Figure 15. Lateral view of left hyoid arch of *Gymnelopsis ochotensis*, UMMZ 202550.

Key to Adults and Late Juveniles of *Gymnelus* and *Gymnelopsis*

1A. Scales present at least on posterior portion of tail (*Gymnelopsis*) 6
1B. Scales absent (*Gymnelus*) 2
  2A. Preoperculomandibular pores five or six; suborbital, interorbital and occipital pores absent; postorbital pores two; vertebrae 88–93; deep shelf areas in Okhotsk and western Bering seas .... *Gymnelus pauciporus* n. sp.
  2B. Preoperculomandibular pores eight (rarely seven or nine); suborbital pores 6–11, occipital pores 2–5, postorbital pores usually four 3
    3A. Vomerine and palatine teeth absent; interorbital pore(s) present; dorsal fin origin extending from vertical with pectoral fin base to vertical 15–20 percent pectoral fin length posterior to pectoral base; intertidal areas of Aleutian and Kurile Islands (and probably adjacent coastal mainlands) .... *Gymnelus popovi* (Taranets and Andriashev)
    3B. Vomerine and palatine teeth usually present (absent on both bones in 1% of present sample); interorbital pore usually absent (present in 3% of sample); dorsal fin origin behind vertical 25 percent pectoral fin length posterior to pectoral base; subtidal habitats (intertidal only in high Arctic; absent from Aleutian and Kurile Islands intertidal 4
      4A. Predorsal length 18–36% standard length ($\bar{x}$ = 30%); dorsal fin origin extending from vertical through posterior margin of pectoral fin to 1.5 pectoral fin lengths behind posterior margin of pectoral; 3–14 free dorsal fin pterygiophores; vertebrae 90–105 ($\bar{x}$ = 98); body pale, usually with 13–16 dark vertical bars; bars on tail always extending from dorsal fin base to anal fin base; pectoral B/L ratio 25–39% ($\bar{x}$ = 31%); usually in deep (50–400 m) shelf areas of Kara and Barents seas, Iceland, Greenland and Arctic Canada .... *Gymnelus retrodorsalis* Le Danois
      4B. Predorsal length 15–22% standard length ($\bar{x}$ = 18.5%); dorsal fin origin extending from 1/3 pectoral fin length behind vertical with pectoral base to a vertical through posterior margin of pectoral fin; 0–2 free dorsal fin

pterygiophores; pectoral B/L ratio 26–60% ($\bar{x}$ = 43%); high Arctic, Bering or Okhotsk seas 5

5A. Vertebrae 85–95 ($\bar{x}$ = 90.4); pectoral B/L ratio 29–46% ($\bar{x}$ = 38%); pectoral rays usually 10–11; body and tail with 12–16 dark bars running to lateral line, rarely with heavy, dark, reticulate pigmentation on body (if so tail bars run below lateral line); deep shelf areas (usually 40–200 m) in Okhotsk, Bering, Beaufort and all Siberian Arctic seas except White Sea; females mature at 70–80 mm .... *Gymnelus hemifasciatus* Andriashev

5B. Vertebrae 92–105 ($\bar{x}$ = 97.9); pectoral B/L ratio 39–60% ($\bar{x}$ = 50%); pectoral rays usually 11–13; body colouration highly variable, when barred, pigmentation always runs below lateral line; shallow depths (intertidal to about 50 m usually) in Greenland, Canada, Alaska, northern Bering sea, Chukchi, East Siberian and Laptev sea; females usually mature at 110–120 mm .... *Gymnelus viridis* (Fabricius)

6A. Suborbital and occipital pores absent, postorbital pores two, branchiostegal rays six .... *Gymnelopsis ocellatus* Solatov

6B. Suborbital and occipital pores present, postorbital pores 3–4, branchiostegal rays five 7

7A. Vertebrae less than 100; dorsal fin rays less than 90, anal fin rays less than 85; gill slit entirely above pectoral fin base or extending ventrally to opposite first or second pectoral ray; gill rakers 9–10; precaudal vertebrae 16–18 .... *Gymnelopsis brevifenestratus* n. sp.

7B. Vertebrae 107–114; dorsal fin rays 90 or more; anal fin rays more than 85; gill slit extending below upper margin of pectoral fin; gill rakers 12–14; precaudal vertebrae 18–23 8

8A. Preoperculomandibular pores five or six; predorsal length 23-33% standard length; dorsal fin origin always behind vertical with posterior margin of pectoral fin; scales covering entire body and tail; large black spot on pectoral fin .... *Gymnelopsis ochotensis* (Popov)

8B. Preoperculomandibular pores seven; predorsal length 16% standard length; dorsal fin origin in front of vertical with posterior margin of pectoral fin; scales only as small patch on posterior 2/3 of trail; no black spot on pectoral fin .... *Gymnelopsis brashnikovi* Soldatov

Systematics

The species of *Gymnelus* and *Gymnelopsis* possess a confusing array of both primitive and derived characters, but are structurally quite similar. Although few non-overlapping characters distinguish the genera, both exhibit trends in a few other character states, summarized in Table 1, which support the validity of these genera.

Gymnelus Reinhardt

Ophidium Fabricius 1780: 141
Gymnelus Reinhardt 1834: 4; Reinhardt 1837a: xxi (type species: *O. viride*, by monotypy)
Gymnelis Reinhardt 1837b: 37, 49; Reinhardt 1838: 116, 131
Cepolophis Kaup 1856a: 96 (type species: *O. viride*, by original designation)
Gymnelichthys Fischer 1885: 60, pl. 2, fig. 9 (type species: *G. antarcticus* by monotypy)
Nemalycodes Herzenstein 1896: 14 (type species: *N. grigorjewi* by monotypy)
Commandorella Taranets and Andriashev 1935: 267–270, fig. 1 (type species: *C. popovi* by original designation)

Description. Body elongate, subcircular in cross-section, its greatest depth variably immediately behind pectoral fin or midway between its base and anus in gravid females. Tail laterally compressed, more so in juveniles than adults, very attenuated, tapering to blunt tip; posteriorly tail more compressed than immediately behind anus. Head subcircular in cross-section in juveniles, more dorsoventrally flattened in adults. Largest males with wider heads than females due to greater development of adductor mandibulae muscles (Andriashev, 1937, Figs. 21, 25). Maximum head height (behind eyes) changing little with growth in each species; head height 33–52% head length. Eye circular, entering dorsal profile of head when viewed laterally in adults and juveniles; eye diameter larger in percent head length in juveniles than adults. Snout, when viewed laterally, steeper in juveniles than adults due to prominence of larger eyes. Upper jaw extending to middle of eye in juveniles or behind posterior margin of eye in adults; adult males with longer upper jaws than females. Mouth terminal; upper lip slightly overhanging lower. Lips fleshy, upper lip rarely adnate to snout in *G. viridis* and *G. hemifasciatus*, free of snout in other species. In adnate-lipped specimens, anterodorsal section of upper lip curves downwardly and fuses into lower part of lip either at snout tip or to one side. Lower lip adnate to chin, with fleshy fold anteriorly. Very weak symphyseal knob formed at dentary juncture in adults of some species. No mental crests formed on anteroventral edge of dentary. Nostrils unpaired, tubular. Teeth on jaws small, conical, blunter in adults than juveniles, in two or three irregular rows anteriorly on premaxillae, single row posteriorly; in two rows anteriorly on dentray, single row posteriorly; no teeth on maxillae. Teeth on vomer and palatines in most specimens of all species except *G. popovi*, in which they are always absent. Palatal membrane (valve) well developed, mandibular membrane low, not extending as far posteriorly as palatal membrane. Palatal sensory papillae usually densest around vomer and in a line extending from vomer posteriorly; in less dense, scattered lines distal to this central line. Gill rakers shorter, more slender and more pointed in juveniles than in adults, becoming more triangular in oldest fish; without denticles; rakers thicker at bases in young fish. Gill raker number individually variable, total number on lower limb expressed in early juveniles. Gill arches four, space between all four; space restricted to lower half of last arch. Gill slit restricted, usually longer in very young fish than in adults, inclined anteroventrally from vertical. Opercular lobe usually continued anteriorly above, forming a blunt, posterior projecting flap. In some species a skin fold on body forms a siphon for passage of water with posterior opercular flap. Dorsal and anal fins long, low, confluent with caudal fin; greatest height of unpaired fins at midpoint of fin length. Origin of dorsal fin extending from directly above pectoral base to about 1.5 head lengths behind pectoral fin base. Anal fin origin 1.4–1.6 head lengths behind pectoral base. Dorsal fin often embellished with ocelli in adults of all species; about as often absent as present; independent of sex. Anal fin becoming black in adult males, never black in females. First dorsal fin ray a true spine, remaining dorsal and all anal fin rays soft rays. Caudal fin rays 9–12: 1–3 rays associated with epural, 7–9 rays associated with hypurals. Pectoral fins small, rounded, with delicate, scaleless membrane; membrane thicker in adults than juveniles; with 9–14 rays. Pelvic fins, facial cirri or papillae and scales absent. Body lateral line mediolateral, complete (or incomplete (?) in *G. pauciporus*) (Andriashev, 1954), composed of free lateralis organs (Springer and Freihofer, 1976: 15–16; Peden and Anderson, 1978), not enclosed within a canal. Independent, dorsal branch of lateral line running from just dorsoposterior opercular lobe along base of dorsal fin to short distance behind vertical with anus; neuromasts very difficult to detect in most specimens. Cephalic lateralis canals opening in small, rounded pores (Fig. 12), with paired preoperculomandibular canal on each jaw extending up cheek; paired supraorbital canal running from in front of nostril, across interorbital space, to behind eye; paired postorbital canal extending from behind eye to upper edge of operculum; paired suborbital canal extending from anteroventral margin of eye to its posterodorsal margin and unpaired occipital (supratemporal) canal running across nape. Number of pores in most canals species-specific, highly variable in others, especially suborbital. In metamorphosing fish, pores at extremes of each canal open first; for example, in preoperculomandibular canal, pores at jaw tip and top of gill cover develop before others. Pseudobranchial filaments well developed, about one eye diameter in length. Pyloric caeca two, blunt and indistinctive in adults, longer and more spindle-shaped in juveniles. Branchiostegal rays usually six; in some species an aberrant few had five or seven. Vertebrae amphicoelus and asymmetrical. Very small, pointed genital papilla developed in both sexes posterior to anus.

Etymology. From the Greek γυμνος (naked) and ενχελυς (eel) referring to absence of scales in generic type (*G. viridis*). Gender, masculine.

Gymnelus viridis (Fabricius, 1780)
Figures 12A, 16

Ophidium viride Fabricius 1780: 141–142 (original description; no illustration, no specimen preserved); Ross 1826: 110.

Ophidium unernak Lacépède 1800: 280, 282.

Gymnelus viridis (Fabricius). Reinhardt 1834: 4; Reinhardt 1837a: xxi; McAllister and Rees 1964: 106; Norman 1966: 479; Andriashev 1973: 540–541; Gosztonyi 1977: 196 (partim).

Gymnelis viridis (Fabricius). Reinhardt 1837b: 37, 49 (improper emendation xxi); Reinhardt 1838: 116, 131; Richardson 1855: 21–26, pls. 29, 30; Kaup 1856b: 156; Krøyer 1862: 258–266; Günther 1862: 323, 324; Walker 1862: 67; Gill 1864: 261, 262; Malmgren 1865: 514–516; Günther 1877a: 294; Günther 1877b: 476; Bean 1879: 112; Collett 1880: 123–125 (partim), pl. 4, fig. 32; Bean 1882: 244 (partim), 268, 269, 271; Jordan and Gilbert 1882: 789; Murdoch 1885: 131; Günther 1887: 82; Lütken 1887: 125, 126; Jordan and Evermann 1896: 481; Goode and Bean 1896: 313; Jordan and Evermann 1898: 2477, figs. 864a-c; Jordan and Gilbert 1899: 485 (partim); Lütken 1899: 18; Knipovich 1901: 75–76 (partim); Collett 1905: 142; Gratsianov 1907: 433 (partim); Evermann and Goldsborough 1907: 344–345 (partim); Knipovich 1907: 39, 40 (partim); Knipovich 1908: 1–16 (partim), figs. 3–4; Kendall 1909: 214, 244; Ehrenbaum 1909: 311, fig. 111; Jensen 1910: 13; Halkett 1913: 115; Hofsten 1919: 61–64, fig. 15 (partim), 88, 89, 93, 94, 97, 101, 110, 118–120; Jordan, Evermann and Clark 1930: 477; Popov 1933: 159, 164–166 (partim); Vladykov 1933: 36

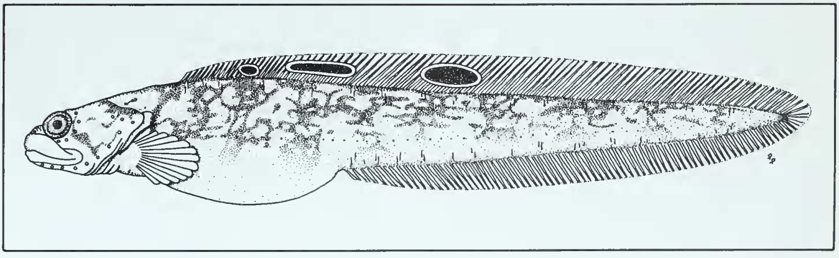

Figure 16. *Gymnelus viridis*: adult female, 152 mm SL, NMC 77-1259, from Arctic Canada.

(partim); Vladykov and McKenzie 1935: 110; Taranets 1937: 165 (partim); Andriashev 1937: 71 (partim); Jensen 1938 (fiche only, partim), figs. 2, 3; Okada 1938: 260 (partim); Andriashev 1939a: 51 (partim); Andriashev 1939b: 132; Hildebrand 1939: 12; Suvorov 1948: 540; Hildebrand 1948: 111; Andriashev 1948: 91, 93 (partim); Dunbar and Hildebrand 1952: 123; Ekman 1953: 139, 178 (partim); Walters 1953a: 4; Walters 1953b: 11–12 (?); Wilimovsky 1954: 288 (partim); Andriashev 1954: 260–262 (partim), fig. 135, tab. 10 (partim); Walters 1955: 308; Matsubara 1955; 780, 781 (partim); Backus 1957: 304; Barsukov 1958: 140; Wilimovsky 1958: 92; Bailey et al. 1960: 29; McAllister 1960a: 33; McAllister 1960b: 14; Makushok 1961: 6, 21, 26, 27; Ellis 1962: 188; Leim and Scott 1966: 317, Bailey et al. 1970: 29; Klimaj and Rutkowicz 1970: sect. 303; Quast and Hall 1972: 13 (partim); Fedorov 1973: 57; Legendre et al. 1975: 9; McAllister 1977: 55, 61; Green and Steele 1977: 85, tab. 3; Carey 1978: 229–231 (partim).

Ophidium stigma Lay and Bennett 1839: 64, tab. 20, fig. 1; Richardson 1836: 273; Walters 1955: 308.

Cepolophis viridis Kaup 1856a: 96

Gymnelis pictus Günther 1862: 324, 325

Gymnelis stigma (Lay and Bennett). Günther 1862: 325; Bean 1882: 262; Jordan and Gilbert 1882: 789; Jordan and Evermann 1898: 2477, 2478; Jordan and Gilbert 1899: 485, 486; Evermann and Goldsborough 1907: 345; Gratsianov 1907: 433 (partim); Halkett 1913: 115; Jordan, Evermann and Clark 1930: 477; Taranets 1937: 165; Makushok 1961: 6, 16, 17.

Gymnelis picta Günther 1881: pl. 2, fig. B; Günther 1887: 81.

Gymnelichthys antarcticus Fischer 1885: 60, pl. 2, fig. 9; Norman 1938: 81; McAllister and Rees 1964: 106.

Maynea stigma Jordan and Evermann 1896: 14.

Gymnelis bilabrus Andriashev 1937: 72, 73, pl. 2, figs. 20–22. Taranets 1937: 165; Andriashev 1939a: 51; Andriashev 1954: 260, 261, 265, 266, fig. 140, 141, table 10; Wilimovsky 1954: 288; Quast and Hall 1972: 13; Fedorov 1973: 57; Lindberg 1974: 207, fig. 799.

Gymnelopsis stigma (Lay and Bennett). Wilimovsky 1954: 288; Wilimovsky 1958: 92; McAllister 1960a: 34; Quast and Hall 1972: 13; Fedorov 1973: 57.

Remarks. Although Lay and Bennett (1839) preserved no specimen of *Ophidium stigma* and their description and sketch are of little diagnostic value, this name (and its other combinations) is entered in the synonymy of *Gymnelus viridis*. Lay and Bennett's sketch and the size given for the fish reveal the typical barred and spotted colour pattern possessed only by young *G. viridis* found throughout the Arctic. The spots were apparently mistaken for scales, a fact first suggested by Jordan and Evermann (1898). None of the scaled species have yet been taken in the Bering Sea (type locality of *O. stigma* is Kotzebue Sound, Alaska). Of the characters Andriashev (1937) used to distinguish *Gymnelus bilabrus* from other species, only the structure of the upper lip in combination with other differences might be used to separate this form from *G. viridis*. Other differences do not exist (Table 2). The value of the adnate upper lip as a taxonomic character is highly questionable as one specimen of two *G. viridis* caught in the same haul in southwest Greenland possessed a completely adnate upper lip; as did those from the Bering Sea. Several *G. hemifasciatus* had partially adnate upper lips as well. The condition of the upper lip in two or more of the Bering Sea specimens seems to be an artifact of preservation, this due to the thicker, looser skin in these large specimens. Oshima's (1957) record of *G. viridis* from the central Japan Sea, judging from other accounts in his paper, must be erroneous.

Neotype. Herein designated: a male, 147 mm standard length (SL), ZMUC P761096, specimen number 93a of J. Reinhardt; southwestern Greenland, collected by Vahl, 24 October 1829.

Diagnosis. *Gymnelus viridis* is distinguished from all other species in the genus by the following combination of characters: vertebrae 92–105 ($\bar{x}$ = 97.9, standard deviation (SD) = 1.97, N = 170); pectoral B/L ratio 39–60% ($\bar{x}$ = 50%, N = 37) in specimens over 75 mm SL; free dorsal fin pterygiophores 0–2; dorsal fin origin in front of or touching vertical through posterior margin of pectoral fin; branchiostegal rays usually six; pectoral rays 10–14 (usually 11–13); vomerine and palatine teeth usually present in metamorphosed fish; following cephalic lateralis pore counts are from fully developed fish (greater than about 70 mm SL): preoperculomandibular pores 7–8 (almost always eight); suborbital pores 5–11 (usually 6–8); interorbital pore almost always absent (present in seven fish); postorbital pores 2–5 (usually four); occipital pores 2–5 (usually two or three); females usually mature at about 110–120 mm SL.

Description. Counts and measurements are given in Table 2. Body elongate, becoming wide as head in largest specimens (over about 220 mm SL). Head roughly ovoid, dorsal profile when viewed laterally with bluntly rounded snout in youngest specimens, becoming more acute in late juveniles, then becoming bluntly rounded in largest fish due to great expansion of snout with age. Head more dorsoventrally flattened in adults than juveniles. Head width 54.3–70.4% head length (HL) ($\bar{x}$ = 62.3%) for 40 adult males measured; head width 39.7–63.6% HL ($\bar{x}$ = 48%) for 42 females. Head length as percent SL smaller in adult females than adult males (Fig. 17). A t-test for significance in difference of the ratio of HL to SL (arcsine transformed) for males versus

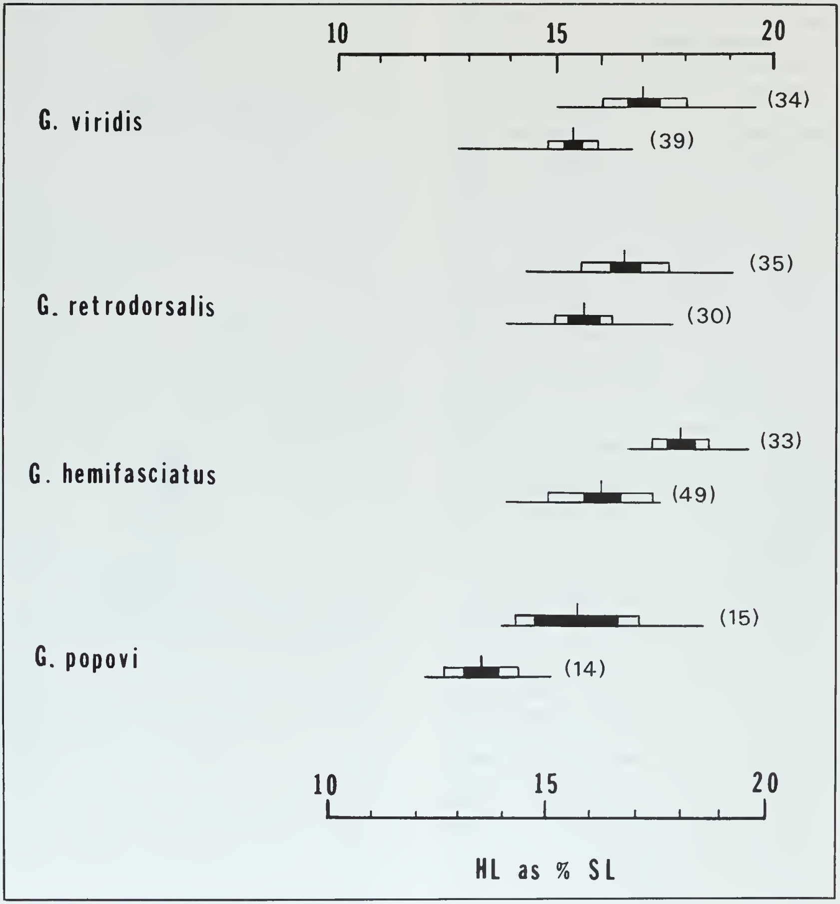

Figure 17. Head length (HL) as percent standard length (SL) in four species of *Gymnelus*. Of two graphic symbols for each species, males upper, females lower. Graphics after Hubbs and Hubbs (1953). Sample sizes for each in parentheses.

females gave a value of 2.03, significant at $p<.05$ with 71 degrees of freedom. Eye diameter 20.1–35.9% HL, ratio decreasing with increasing size. A linear regression of the ratio of eye diameter to head length versus head length gave a correlation coefficient (r) of -0.871, N=70. Body depth at anal fin origin 7.4–11.3% SL, ratio poorly correlated with size (r = .176, N = 39). Upper lip with partial or complete fusion to snout tip in four specimens, with free fold, as in other species, in all other fish (N = 279). Lower lip with fleshy lobe anteriorly; adnate to chin tip. Upper jaw length 41.9–57.6% HL ($\bar{x}$ = 50.0%) for 31 adult males; upper jaw length 34.6–46.9% HL ($\bar{x}$ = 40.8%) for 25 adult females. Upper jaws grow longer in males than in females but this difference, as percent head length, is observed since females have shorter heads than males (Fig. 17). Thus there is no significant difference in jaw lengths between sexes as percent of head length in fish larger than about 190 mm SL. A linear regression of head length vs. standard length showed head length to be a good measure of absolute growth in the species (r = .894, N = 89). Teeth on jaws small; posterior teeth slightly recurved inwardly. Males generally have fewer teeth in anterior patches on both jaws than females, but since these teeth are so few and variable, differences were not statistically detectable. No sexual differences in numbers of vomerine or palatine teeth. Usually 4–8 teeth present on vomer in an irregular patch. Palatine teeth usually in a single row, inwardly recurved. Teeth absent on palatines in only six fish examined, absent on both palatines in only one adult specimen (teeth first appear at lengths of about 50–60 mm SL). Dorsal edge of operculum continued anteriorly about half eye diameter, slightly less in very small fish; dorsoposteriormost tip of operculum with weakly developed strut having nearly squared off edges. Gill slit usually extending to opposite 4–6th pectoral fin ray in late juveniles and adults; to opposite 6–9th ray in fish less than about 60 mm SL. Gill raker number increases with growth. Increase takes place at a slower rate on the upper limb (epibranchial) than on lower limb (ceratobranchial); maximum number on upper limb expressed by about 120–130 mm SL; on lower by about 80–90 mm SL. Gill rakers longer in largest adults; dorsalmost four rakers on lower limb overlap bases of adjacent rakers in fish less than 75 mm SL, all rakers overlap bases of adjacent rakers in fish over about 110 mm SL. Pseudobranchial filaments usually 6–8. Branchiostegal rays five on one side, six on the other in one specimen, seven on both sides in two specimens, but six on both sides in all others (201 specimens). Lateral line with about 30 neuromasts anterior to vertical passing through anus. Dorsal branch of lateral line running to about 1–1½ head lengths posterior to vertical through anus; composed of 12–16 neuromasts. Cephalic lateralis pore pattern usually complete (Fig. 12). Preoperculomandibular pores usually eight (seven on one side, eight on the other in two fish; nine on one side, eight on the other in one); pores fully developed by about 50 mm SL. Suborbital pores usually six or seven, often with two or three small pores developed where one normally opens; less than five pores only in youngest fish (less than about 60 mm SL). Postorbital pores usually four; pores develop by about 45–50 mm SL. Interorbital pore present in eight specimens 25–140 mm SL, its presence apparently not associated with age; all eight, however, were collected in central Arctic Canada. Two anterior supraorbital pores, as in all *Gymnelus* species, one in front of nostril tube, the other posterodorsal to nostril; two specimens examined had three pores in nostril vicinity; these had no interorbital pore; pores developed in smallest fish examined (37 mm SL). Occipital (supratemporal) pores about as often two as three; when two, central pore missing; occasionally four or five pores present; pores develop by about 65–70 mm SL.

Dorsal fin origin 50–90 percent pectoral fin length posterior to vertical with pectoral base. Dorsal origin associated with vertebrae 2–5, anal fin origin associated with vertebrae 18–24. One to three anal fin pterygiophores anterior to haemal spine of first caudal vertebra, none without associated fin ray. Zero or one free dorsal fin pterygiophore usually, very rarely two. Caudal fin with 1–3 rays associated with epural, 7–9 rays with hypurals. Pectoral fin small, broadly rounded, tips of lowermost fin rays slightly exserted from membrane; usually 11–13 rays (Fig. 18). Precaudal vertebrae usually 19–22 (Fig. 19). Skin thick, covering bases of fins, noticeably thicker and more wrinkled in largest fish, scales absent. Maximum size 256 mm SL.

Colouration highly variable, three basic patterns exhibited: 1) monotone brown to green, 2) banded with bluish stripes on pale, yellowish-orange background, or yellowish banding on

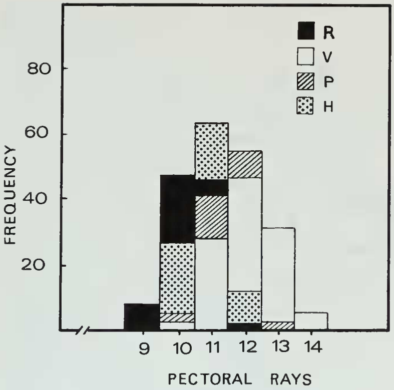

Figure 18. Percent frequency of pectoral fin rays in four species of *Gymnelus*. Abbreviations: R, *G. retrodorsalis*; V, *G. viridis*; P, *G. popovi*; H, *G. hemifasciatus*.

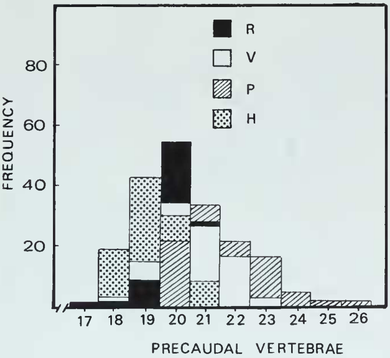

Figure 19. Percent frequency of precaudal vertebrae in four species of *Gymnelus*. Graphics after Figure 18.

greenish-brown background, or 3) variously mottled with white or yellowish reticulations on a greenish-brown to red background. Mottling takes the form of broad swathes or spots in irregular patches to fine lines in a banding pattern with about 15–20 vertical bands present. Youngest fish rarely monotone, usually with mottled pattern; adult females more often mottled than monotone; blue banded pattern least common. Emery (1973) reported orange cheeks, yellow abdomen and blue-black unpaired fins in specimens observed while scuba diving in Arctic Canada. Ocelli in dorsal fin, when occurring, black or bluish black, ringed in white (or yellow?). Ocelli appear in juveniles at about 60–70 mm SL and occurred in 42% of 223 fish examined over 70 mm SL. The sex ratio of fish with ocelli was 56% males, 44% females. Most fish have 1–3 ocelli; only two had four ocelli, one had six. In young lightly pigmented fish, peritoneum showing through body wall makes abdomen appear dark blue. Anal fin in adult males, over about 75 mm SL, black or blue black, females with light (yellow to light brown) anal fin.

Distribution. Known from Scoresby Sound, northeastern Greenland, western Greenland and across Canadian Arctic archipelago to Beaufort, Chukchi, Bering, East Siberian, Laptev and Barents seas. South in eastern Canada along Labrador coast to off Newfoundland, Nova Scotia and mouth of Saguenay Fjord, St. Lawrence River. South in Bering Sea to off Islands of Four Mountains, Aleutian Islands in the east and at least southern Anadyr Gulf in the west (Fig. 20). Habitat muddy bottoms, often associated with brown kelp (*Laminarians*), most captures are from intertidal to about 50 m. Maximum depth 256 m in Frobisher Bay, Baffin Island, Canada (McAllister et al., 1981). A description of a typical Arctic habitat in which *G. viridis* was the second most abundant fish observed by scuba divers is given in Green and Steele (1977). Andriashev (1939b) and McAllister (1977) also reviewed typical Arctic habitats and associated fauna and flora. The collection of *G. viridis* at Alert, Ellesmere Island (82°29′N) reported by Walters (1953a) place it among the northernmost fishes known. This specimen was not located and is probably lost. However, specimen NMC 77–1094 from Robeson Channel at 82°24.0′N, 61°10.0′W verifies the extreme northern limit of this species' range. Bottom temperatures recorded with captures for *G. viridis* range from −1.9°C to about +4.0°C but higher temperatures may be encountered in the southern parts of the range. Andriashev (1948) reports *G. viridis* caught in lowered salinities (27.2–27.7°/₀₀) in the Laptev Sea, but most of those specimens are *G. hemifasciatus*.

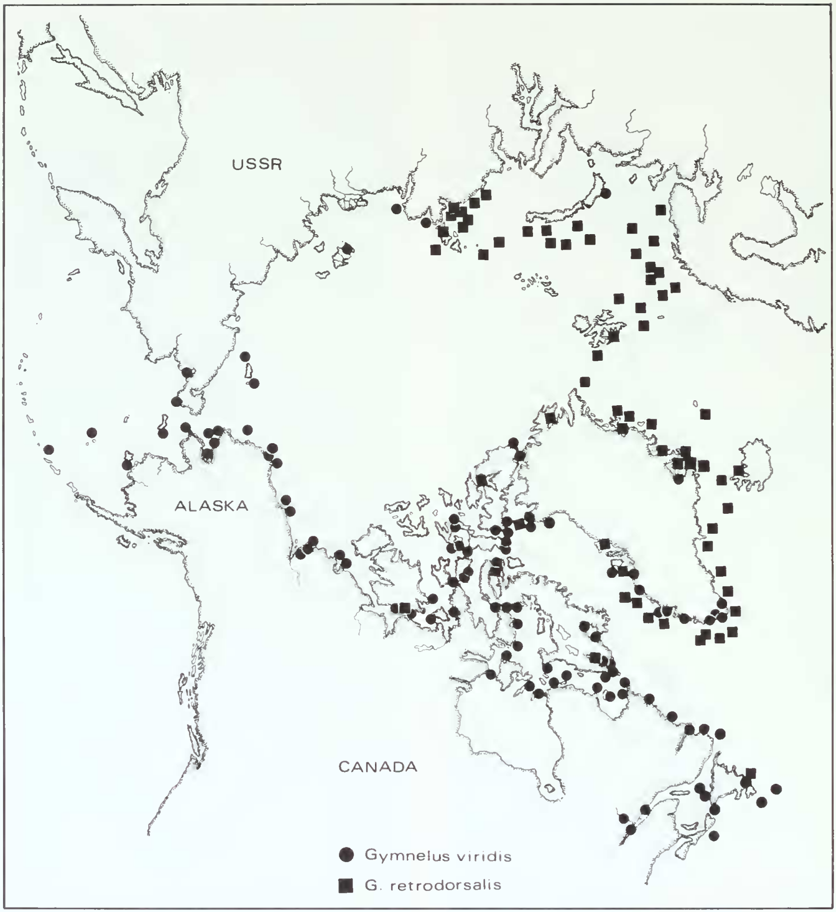

Figure 20. Distribution of *Gymnelus viridis* and *G. retrodorsalis*. One mark may represent more than one collection.

Gymnelus viridis appears to be a semi-circumarctic species. More intertidal or shallow subtidal collecting in the Kara and Barents seas is needed to ascertain how far westward into the Soviet–Norwegian Arctic the species is distributed. Deep water between eastern Greenland and the Barents Sea probably interferes with gene exchange between these populations. Despite its broad range there appear to be no geographically isolated populations, as all areas from which the species has been collected are continuously connected through suitable habitats and depths except the east Greenland–Barents Sea regions. Peden (1979) tested for populational differences among stocks of another eelpout, *Lycodapus mandibularis*, by plotting vertebral numbers for each area concerned. Using this method to help detect populational differences in *G. viridis*, no significant differences among areas were detected (Fig. 21). Some areas were inadequately sampled; very little data is available for this species in the eastern Soviet Arctic or eastern Greenland where it is undoubtedly more abundant than current collections reflect. The uniformity of vertebral numbers in *G. viridis* may be a reflection of the environmental homogeneity of the Arctic, if this is the major determining factor of meristic variation as has been suggested (reviewed in Peden, 1979, and alternatives).

Natural history. Very little has been recorded of the food habits of *G. viridis*. It seems to prefer amphipods, polychaetes, bivalves, mysids and other infaunal invertebrates (Knipovich, 1908; Jensen, 1938; Carey, 1978; pers. observ.). No information exists on age and growth. Females close to spawning contained about 25–35 eggs 3.2–3.6 mm in diameter produced from a single-lobed ovary. One apparently precocious female at 97 mm SL had 31 eggs averaging 3.3 mm in diameter. Larger females (over 150 mm SL) were found with 90–106 eggs 4.1–4.6 mm in diameter. Although the vast majority of specimens have been taken during summer months, spawning appears to be restricted to late summer–early autumn. Large females taken between May and July never had eggs as large as those taken in August through October; no winter or spring-caught females were ripe. Emery (1973) reported pairs of *G. viridis* sharing common burrows under boulders in Arctic Canada. Seals, seagulls, murres, cod and wolf fish have been recorded as predators of *G. viridis*.

Etymology. From the Latin "viridis" (green), alluding to one of the major colour varieties. Vernacular names include "fish doctor" and "unernak" (Inuit) (Legendre et al., 1975).

Gymnelus retrodorsalis Le Danois, 1913
Figure 22

Ophidium chinense (non Linnaeus). Bloch and Schneider 1801: 486 pl. 90, fig. 1 (as *O. imberbe*).

Gymnelis viridis (non Reinhardt). Yarrell 1859: 81, fig.; Collett 1880: 123–125 (partim); Günther 1887: 82; Lütken 1899: 18 (partim); Knipovich 1901: 75–76 (partim); Jensen 1904: 264–265 (partim); Collett 1905: 142–143; Gratsianov 1907: 433 (partim); Knipovich 1907: 39–40 (partim); Knipovich 1908: 1–16 (partim); figs. 1, 2, 5, 6; Johansen 1912: 664, pl. 45, figs. 1–3; Saemundsson 1913: 7; Hofsten 1919: 61–64, 87, 89, 110, fig. 15 (partim); Soldatov 1923: 56 (partim); Knipovich 1926: 113, fig. 76; Esipov 1931: 160; Popov 1933: 159, 164–166 (partim); Jensen 1938 (partim), figs. 1, 4, 5; Saemundsson 1939: 198; Esipov 1939: 882; Esipov 1940: 141; Saemundsson 1949: 53.

Gymnelis retrodorsalis Le Danois 1913: 258–259 (original description; type not designated, no illustration). Le Danois 1914: 16, 58, figs. 5, 22, tab., fig. 1, 2. Andriashev 1954: 260–264, figs. 136, 137, 138, tab. 10; Andriashev 1964: 375.

Gymnelus retrodorsalis. Andriashev 1973: 541. McAllister et al. 1981: 835–838, figs. 2, 5.

Gymnelus viridis (non Reinhardt). Gosztonyi 1977: 196 (partim; ISH specimens).

Remarks. Le Danois' (1913) single specimen of *G. retrodorsalis* was not located after considerable search in North American and European museums, particularly those in French speaking nations (M.-L. Bauchot, pers. comm.) and is probably lost. As with *G. viridis*, a neotype is designated for *G. retrodorsalis* due to the great confusion in the literature between the two species and lack of type material for both.

Neotype. Herein designated: a male, 122 mm standard length (SL); NMC 79-716, Denmark Strait, 65°52′N, 29°20′W, 20–30 March 1979, shrimp trawl in 335–346 m; collected by Marine Research Institute of Iceland, R/V BJARNI SAEMUNDSSON, Sta. 79-21. Gift to the author from Gunnar Jónsson, MRII.

Diagnosis. *Gymnelus retrodorsalis* is distinguished from all other species in the genus by the following combination of characters: vertebrae 90–105 ($\bar{x} = 97.3$, SD = 2.81, N = 108); dorsal fin rays 78–99; anal fin rays 71–84; pectoral B/L ratio 24–39% ($\bar{x} = 30.7\%$, N = 53) in specimens over 80 mm SL; free dorsal fin pterygiophores 3–14; dorsal fin origin behind or touching vertical through posterior margin of pectoral fin; branchiostegal rays usually six; pectoral rays 9–12 (usually 10 or 11); vomerine and palatine teeth always present in metamorphosed fish; following cephalic lateralis pore counts are from fully developed fish (greater than about 70 mm SL): preoperculomandibular pores 7–8 (almost always eight); suborbital pores 0–10 (usually 6–8 except in Kara-Barents seas population); interorbital pore always absent; postorbital pores 2–6 (usually four); occipital pores 0–5 (usually two except in Kara-Barents seas population); females mature at about 90–100 mm SL.

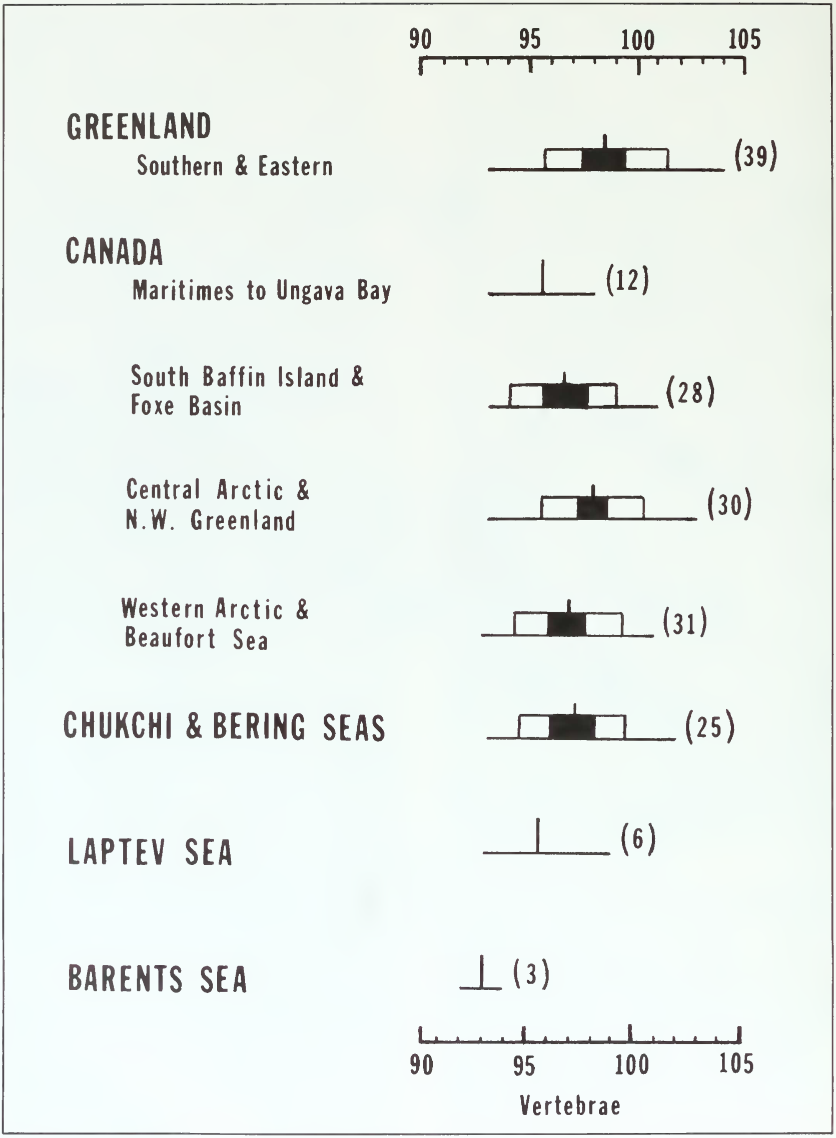

Figure 21. Geographic variation in total number of vertebrae in *Gymnelus viridis*. Sample sizes in parentheses. Graphics after Hubbs and Hubbs (1953).

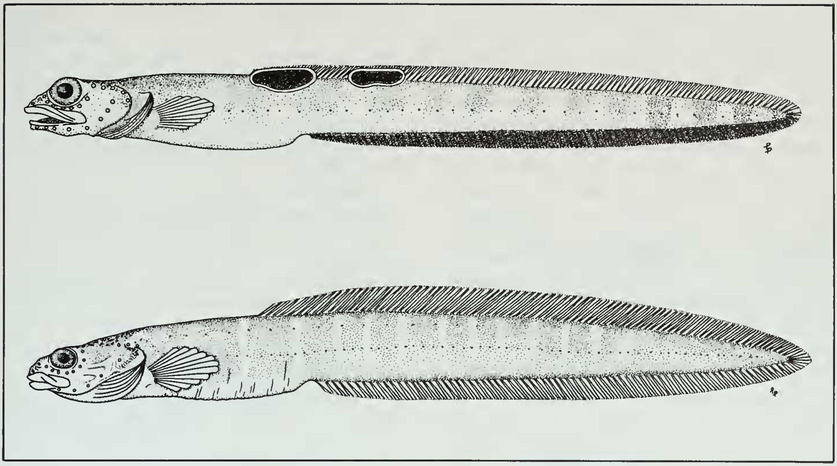

Figure 22. *Gymnelus retrodorsalis*: upper neotype, adult male, 122 mm SL, NMC 79-716, off Iceland; lower, adult female, 92 mm SL, ZMUC P 76192, southwestern Greenland.

Description. Counts and measurements are given in Table 2. Body elongate, becoming wide as head only in gravid females. Head roughly ovoid, dorsal profile when viewed laterally steeper anteriorly in metamorphosing fish, snout becoming more acute in late juveniles, then more rounded and depressed in adults. Head width 48.7-61.7% head length (HL) ($\bar{x}$ = 54.9%) for 24 adult males; head width 42.9-52.4% HL ($\bar{x}$ = 46.5%) for 25 females. Head length as percent SL for both sexes about equal (Fig. 17). A t-test for significance in difference of the ratio of HL to SL (arcsine transformed) for males versus females gave a value of 0.85, not significant at $p<0.4$ with 63 degrees of freedom. Eye diameter 25.2–42.2% HL, ratio subject to great individual variation. A linear regression of the ratio of eye diameter to head length versus head length gave a poor correlation coefficient (r = .0954, N = 48). Body depth at anal fin origin 5.0–8.3% SL, ratio also poorly correlated with length (r = .106, N = 46). Mouth terminal, upper lip usually very slightly overhanging lower in adults; in some specimens regardless of size, lips equal anteriorly. Upper lip with free fold across snout. Lower lip with fleshy fold anteriorly; lip adnate to chin tip. Upper jaw length 40.4–55.5% HL ($\bar{x}$ = 48.9%) for 30 males; upper jaw length 36.6–47.3% HL ($\bar{x}$ = 41.3%) for 16 females. Teeth on jaws with no significant differences in numbers of jaw teeth between sexes. Teeth on vomer in ovoid patch, usually 4–8 teeth present. Palatine teeth blunt, in single row. Teeth present on vomer and palatines in all fish examined over 35 mm SL. Dorsal edge of operculum continued forward less than half eye diameter; dorsoposteriormost tip of operculum rounded in all fish. Gill slit usually extending to opposite second to sixth pectoral fin ray in late juveniles and adults; to opposite fifth to tenth ray in fish less than 70 mm SL. Maximum number of gill rakers on upper and lower limbs developed by about 70–80 mm SL. Gill rakers longer but not more acute in adults than young fish. Dorsalmost five rakers on lower limb overlap bases of adjacent rakers in fish less than 60 mm SL; all rakers overlap bases of adjacent rakers in fish over about 75 mm SL. Pseudobranchial filaments usually 5–7. Branchiostegal rays five on both sides in two specimens, five on one side, six on the other in four, six on both sides in 71 others. Lateral line with about 23–25 neuromasts anterior to vertical with anus. Dorsal branch of lateral line running to about ¾–1 head length posterior to vertical with anus; composed of 17–21 neuromasts. Cephalic lateralis pore distribution subject to greater individual variation than other species of *Gymnelus*. Preoperculomandibular pores usually eight (seven on one side, eight on the other in four specimens, seven on both sides in two); pores develop by about 35–40 mm SL. Suborbital pores usually 6–8, often with two or three pores developing where one normally opens. Suborbital pores more often 0–4 in Kara-Barents seas population (central pores usually not developed in these); six to eight pores also evident in fish from this area; suborbital pores develop by about 60–70 mm SL. Postorbital pores usually four; in Kara-Barents seas population usually two or three; pores develop by about 60–70 mm SL. Interorbital pore always absent. Two anterior supraorbital pores present in all fish examined (to 31 mm SL). Occipital pores usually two, rarely three; about a third of the specimens from Kara-Barents seas population without occipital pores; one of these (ZIL 29453) possesses five pores.

Dorsal fin origin at or behind vertical through posterior margin of pectoral fin. Dorsal fin origin associated with vertebrae 5–15; anal fin origin associated with vertebrae 19–22. One to three anal fin pterygiophores anterior to haemal spine of first caudal vertebra, all with associated fin rays. Three to 14 free dorsal fin pterygiophores, only 18% of sample with less than five. Caudal fin with two rays associated with the epural, 8–10 rays associated with hypurals. Pectoral fin small, rounded, lowermost 6–7 rays slightly more exserted than upper rays; fin membrane thicker in adults than juveniles; usually 10–11 rays (Fig. 18). Pectoral fin base more dorsoventrally constricted than other species, resulting in lower pectoral B/L ratios (Table 2). Precaudal vertebrae usually 20–21 (Fig. 19). Skin thin, delicate, covering unpaired fins, scales absent. Maximum size to 135 mm SL.

Colour light tan to translucent cream with 13–16 brown bars on body and tail running from nape to tail tip, always extending below lateral line. Occasionally dense aggregation of melanophores present on jaws, cheeks, upper part of head and dorsum, dorsal and anal fins and pectoral fin base. Juveniles occasionally with a row of about 11–14 small white spots along base of dorsal fin extending from nape almost to tail tip. Ocelli in dorsal fin, when occurring, black, ringed in white; in neotype ocelli cover back as well as portion of dorsal fin (Fig. 22). Ocelli appear in juveniles at about 60–70 mm SL and occurred in 48% of 92 fish examined over 70 mm SL. The sex ratio of fish with ocelli was 59% males, 41% females. Fish with ocelli usually had 1–3, only two had four ocelli, two had five ocelli and one had six. Anal fin in males over about 75–80 mm SL black, females with light anal fin. D.E. McAllister observed the anal fin of an adult male rapidly turn from dark to light in a shipboard aquarium shortly after capture (McAllister et al., 1981).

Distribution. Known from western Arctic Canada (Dease Strait) and eastern Canada from Axel Heiberg Island to Newfoundland, western and eastern Greenland, Iceland, off Jan Mayen, Spitsbergen and Kara and Barents seas (Fig. 20). Habitat muddy or sandy bottoms, often, perhaps chiefly, associated with shell rubble or gravel in deep shelf-upper slope areas or deep water inlets. Most captures are from about 60–300 m, but it has been taken in 5–9 m in northeastern Greenland and to 481 m off Jan Mayen. Bottom temperatures recorded with captures have ranged from -1.8°C to about +4.0°C. *G. retrodorsalis* is apparently replaced in western Arctic Canada by *G. hemifasciatus* (also a deep-living species), but the two are sympatric in the Kara and Barents seas (Figs. 20, 25). No geographical differences were detected by plotting vertebral numbers, but this needs further evaluation when larger samples are obtained, especially from Arctic Canada (Fig. 23).

Natural history. Females ripen for first spawning at about 90–100 mm SL with about 14–28 eggs 2.9–3.1 mm in diameter. Ripe eggs are reported to be 4.0–4.5 mm in diameter (Andriashev, 1954; McAllister et al., 1981). Spawning appears to occur in late summer or early fall, as in *G. viridis*. Soldatov (1923) reported eggs with embryos near hatching collected 27 August; they were 4.5–4.8 mm in diameter. McAllister et al. (1981) aged a 122 mm fish to 5 years and reviewed temperature and salinity data taken at captures.

Etymology. From the Latin "retro" (behind) and "dorsum" (the back) in reference to the posterior dorsal fin origin. McAllister et al. (1981) coined the vernacular "aurora pout" for this species.

Gymnelus hemifasciatus Andriashev, 1937
Figure 24

Gymnelis viridis (non Fabricius). Bean 1882: 268 (partim); Gilbert 1895: 455 (partim); Lütken 1899: 18 (partim); Gratsianov 1907: 433

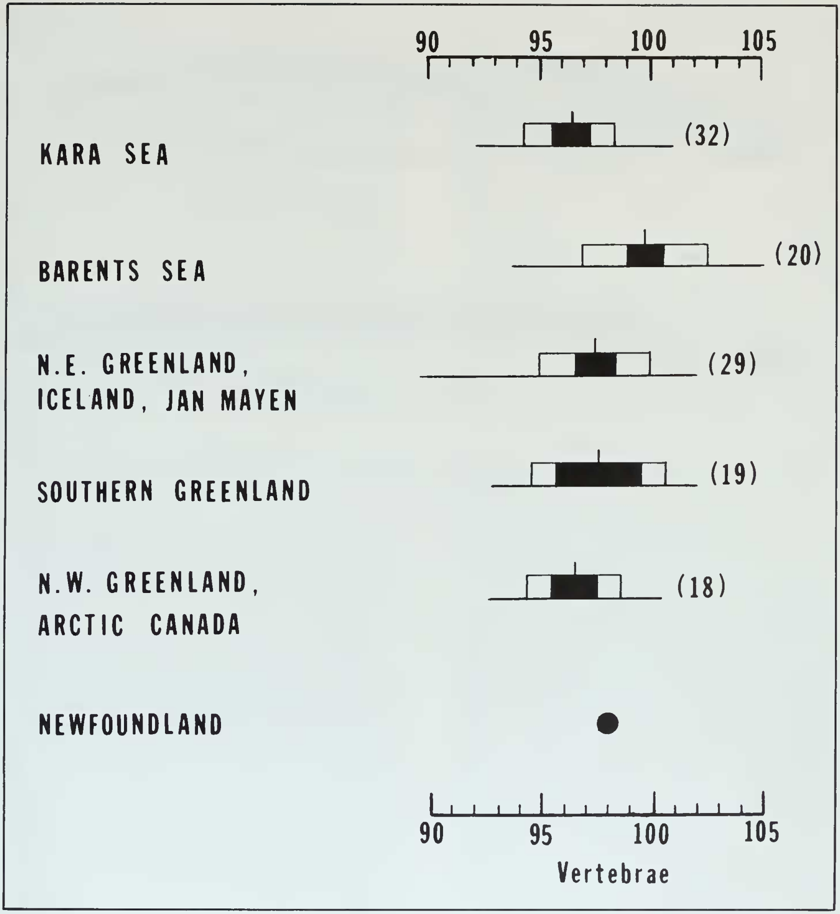

Figure 23. Geographic variation in total number of vertebrae in *Gymnelus retrodorsalis*. Sample sizes in parentheses; single dot represents one specimen. Graphics after Hubbs and Hubbs (1953).

(partim); Popov 1931: 138; Popov 1933: 164–166 (partim); Vladykov 1933: 38 (partim); Andriashev 1937: 71 (partim); Taranets 1937: 165 (partim); Okada 1938: 260 (partim); Andriashev 1939a: 71 (partim); Andriashev 1948: 91, 93 (partim); Shmidt 1950: 122–124, tab. 25; Ekman 1953: 178 (partim); Andriashev 1954: 5, 262 (partim); Wilimovsky 1954: 288 (partim); Bayliff 1954: 5; Matsubara 1955: 780–781 (partim); Walters 1955: 308 (partim); Oshima 1957: 7 (partim); Quast and Hall 1972: 13 (partim); Fedorov 1973: 57; Carey 1978: 229–231 (partim).

Gymnelis viridis morpha *ochotensis* Soldatov and Lindberg 1930: 506–507, tab.

Gymnelis hemifasciatus Andriashev 1937: 73–75, pl. 2, figs. 23, 24 (original description); Taranets 1937: 165; Andriashev 1939a: 51;

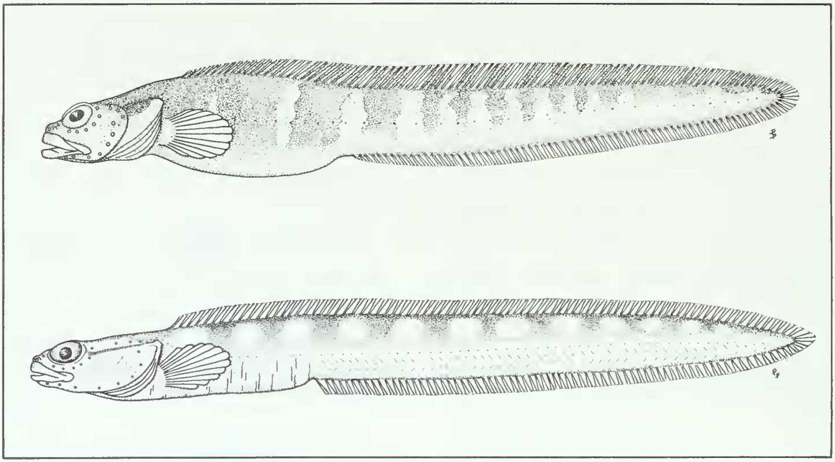

Figure 24. *Gymnelus hemifasciatus*: upper, adult female, 115 mm SL, ZIL 35641, Barents Sea; lower, juvenile female, 65 mm SL, UA 1225, Chukchi Sea.

Andriashev 1954: 260, 261, 264, 265, figs. 139, 141, tab. 10; Ueno 1971: 13; Quast and Hall 1972: 13.

Remarks. In the index, species account and table of measurements Soldatov and Lindberg (1930) listed this species as *Gymnelis viridis* morpha *ochotensis* and stated their three specimens could not be placed in a separate subspecies, as they originally intended but, rather, constituted a "special morph." However, the closing sentence of the account contradicts this (translation mine): "Our collections indicate that this species is encountered in the Okhotsk Sea, where it apparently produces a particular subspecies *ochotensis*." Since these specimens (ZIL 20165, 20166) in fact represent a distinct species, the question of nomenclatural availability arises. According to the International Code of Zoological Nomenclature of 1964 (Article 45e), designations "variety" or "form" (morph) before 1960 are not express statements of infraspecific status. Therefore, Soldatov and Lindberg's *ochotensis* is unavailable if the assumption is made that their closing statement was a lapse, since in three other places "morpha" is clearly indicated. I make this assumption and use the next available name.

Holotype. A female, 96 mm standard length (SL), ZIL 24944, northern Bering Sea, 64°15.5′N, 172°27.0′W, 25 August 1932, dredge in 55 m in gravel, temperature 1.3°C; collected by A.P. Andriashev, R/V DAL'NEVOSTOCHNYKH, Sta. 47 (40).

Paratype. None.

Diagnosis. *Gymnelus hemifasciatus* is distinguished from all other species in the genus by the following combination of characters: vertebrae 85–95 ($\bar{x}$ = 90.4, SD = 2.42, N = 86); dorsal fin rays 82–94; anal fin rays 68–76; pectoral B/L ratio 25–46% ($\bar{x}$ = 37.5%, N = 39) in specimens over 80 mm SL; free dorsal fin pterygiophores 0–2; dorsal fin origin 25–75% pectoral fin length behind vertical with pectoral base; branchiostegal rays usually six; pectoral fin rays 10–12; vomerine and palatine teeth usually present in metamorphosed fish; following cephalic lateralis pore counts are from fully developed fish (greater than about 55 mm SL): preoperculomandibular pores 7–8 (usually eight); suborbital pores 6–9 (usually six); interorbital pore usually absent; postorbital pores 3–5 (usually four); occipital pores 2–3 (usually two). Body and tail usually with 12–16 dark vertical bars, running to lateral line on tail, below it only in some of the largest specimens; females mature at 70–80 mm SL.

Description. Counts and measurements are given in Table 2. Body elongate, wider than head in gravid females. Head roughly ovoid, dorsal profile when viewed laterally most acute in juveniles, becoming more anteriorly rounded and more dorsoventrally flattened in adults than juveniles; snout laterally more rounded in adults than juveniles. Head width 55.7–69.6% head length (HL) ($\bar{x}$ = 61.7%) for 21 adult males; head width 34.0–56.8% HL ($\bar{x}$ = 49.7%) for 17 adult females. Head length of adult females smaller than adult males (Fig. 17). A t-test for significance in difference of the ratio of HL to SL (arcsine transformed) for males versus females gave a value of 2.46, significant at $p<.02$ with 79 degrees of freedom. Eye diameter 25.2–37.3% HL, ratio subject to great individual variation. A linear regression of the ratio of eye diameter to head length versus head length gave a poor correlation coefficient ($r = -.415$, $N = 58$). Body depth at anal fin origin 7.4–10.6% SL, ratio also poorly correlated with length ($r = .047$, $N = 45$). Mouth terminal, upper lip slightly overhanging lower in both juveniles and adults; in many younger fish lips equal. Upper lip usually with free fold across snout, partially adnate to snout in only four specimens examined; lower lip adnate to chin, with small fleshy lobe anteriorly. Upper jaw length 45.9–62.3% HL ($\bar{x}$ = 51.4%) for 20 adult males; upper jaw length 38.1–49.5% HL ($\bar{x}$ = 43.5%) for 27 adult females. Teeth on jaws with outer rows inwardly recurved, no significant differences in numbers of jaw teeth between sexes. Usually 3–6 teeth present on vomer in round part. Palatine teeth blunt, in single row. Teeth develop on vomer and palatines between about 35–50 mm SL, palatine teeth develop last. Only one fish over 50 mm SL lacked palatine teeth, another lacked teeth on both vomer and palatines. Dorso-posteriormost edge of operculum continued anteriorly less than half eye diameter; in some large males, gill slit not continued forward dorsally. Gill slit usually extending ventrally to opposite second to sixth pectoral fin ray in late juveniles and adults, to opposite fifth to eighth ray in fish less than 70 mm SL. Maximum number of gill rakers on upper limb develop by about 80–95 mm SL, by about 70–80 mm SL on lower limb. Outer gill rakers on lower limb overlap bases of adjacent rakers in all fish over about 60 mm SL. Pseudobranchial filaments usually five or six. Branchiostegal rays five on both sides in eight specimens, five on one side, six on the other in five specimens, seven on one side, six on the other in one fish, six on both sides in all others (64 specimens). Lateral line with about 20–25 neuromasts anterior to vertical with anus. Dorsal branch of lateral line running to about 1.5 head lengths posterior to vertical with anus; composed of 16–19 neuromasts. Cephalic lateralis pore distribution not highly variable, system usually complete. Preoperculomandibular pores usually eight (six on both sides in one fish 107 mm SL); pores develop by about 35–40 mm SL. Suborbital pores usually six or seven, rarely with two opening where one normally develops; pores open by about 60–70 mm SL. Postorbital pores usually four (five on one side, four on the other in three late juvenile or adult fish, three on both sides in one adult); pores develop by about 50–60 mm SL. Interorbital pore present in only one specimen examined (106 mm SL). Two anterior supraorbital pores present in all specimens examined (to 28 mm SL). Occipital pores usually two or rarely three; one in four fish, none in three late juvenile or adults; pores develop by about 35–40 mm SL.

Dorsal fin origin 25–75 percent pectoral fin length posterior to pectoral base. Dorsal origin associated with vertebrae 2–3; anal fin origin associated with vertebrae 18–21. One or two anal fin pterygiophores anterior to haemal spine of first caudal vertera, none without associated fin ray. Zero to two free dorsal fin pterygiophores. Caudal fin with 1–2 rays associated with epural, eight rays associated with hypurals. Pectoral fin small, rounded, ventralmost 5–7 rays slightly more widely exserted than dorsalmost rays; fin membrane thin, delicate, slightly thicker in large adults than smaller fish; usually 10–11 rays (Fig. 18). Precaudal vertebrae usually 18–20 (Fig. 19). Skin thin, covering unpaired fins, scales absent. Maximum size 140 mm SL.

Colouration in life unknown; in alcohol body pale with 12–16 dark bands running from nape to tail tip. Bands either dissociate to heavy reticulation or expand across body to greatly reduce light areas there and on anterior portion of tail; bars on tail descend below lateral line only in some of the largest fish (Fig. 24; Andriashev, 1937, Fig. 23), most of these are males. Females commonly with greatly restricted lateral banding and high, light ventral surface (probably yellow). Juveniles more lightly pigmented than adults. Dorsal surface of head with fine, dark reticulation in late juveniles and adult females (Andriashev, 1937, Fig. 24), often descending to cheeks, snout and lips. Ocelli black, ringed in lighter colour, when occurring. Ocelli appear in juveniles at about 50–60 mm SL and occurred in 38% of 69 fish examined over 60 mm SL. The sex ratio of fish with ocelli was 42% males, 58% females. Fish with ocelli usually have 1–3; one was found with five ocelli, one had eight. Anal fin in males over about 75–85 mm SL black, anal fin in females light.

Distribution. Known from western Arctic Canada (Dease Strait) and all Arctic Seas westward to Barents Sea, throughout Okhotsk and Bering seas and northern Gulf of Alaska (Fig. 25). Habitat usually mud and gravel bottoms of inner and outer shelf. Most captures are from about 40–80 m, but there are numerous records shoaler than 20 m, minimum recorded depth is an intertidal collection in the Laptev Sea, the deepest is 200 m in Kronotskiy Bay, Kamchatka. Bottom temperatures recorded with captures are meager, ranging from about −1.8°C to about +2.0°C. No populational differences were detected by plotting vertebral numbers, but larger samples are needed from all localities to further test this (Fig. 26).

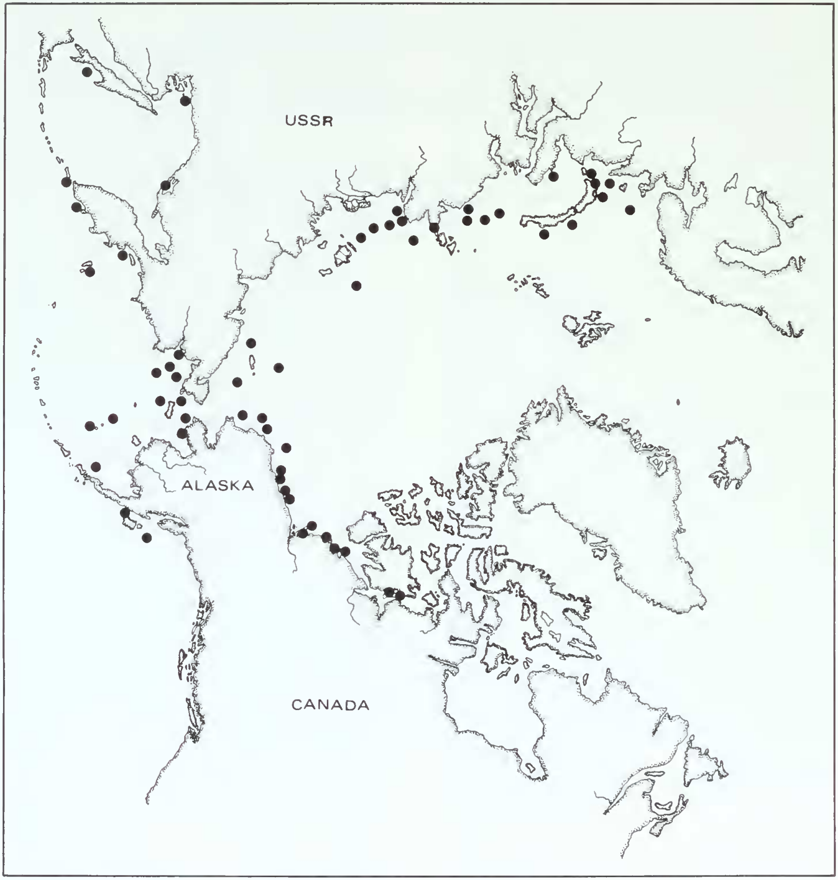

Figure 25. Distribution of *Gymnelus hemifasciatus*. One mark may represent more than one collection.

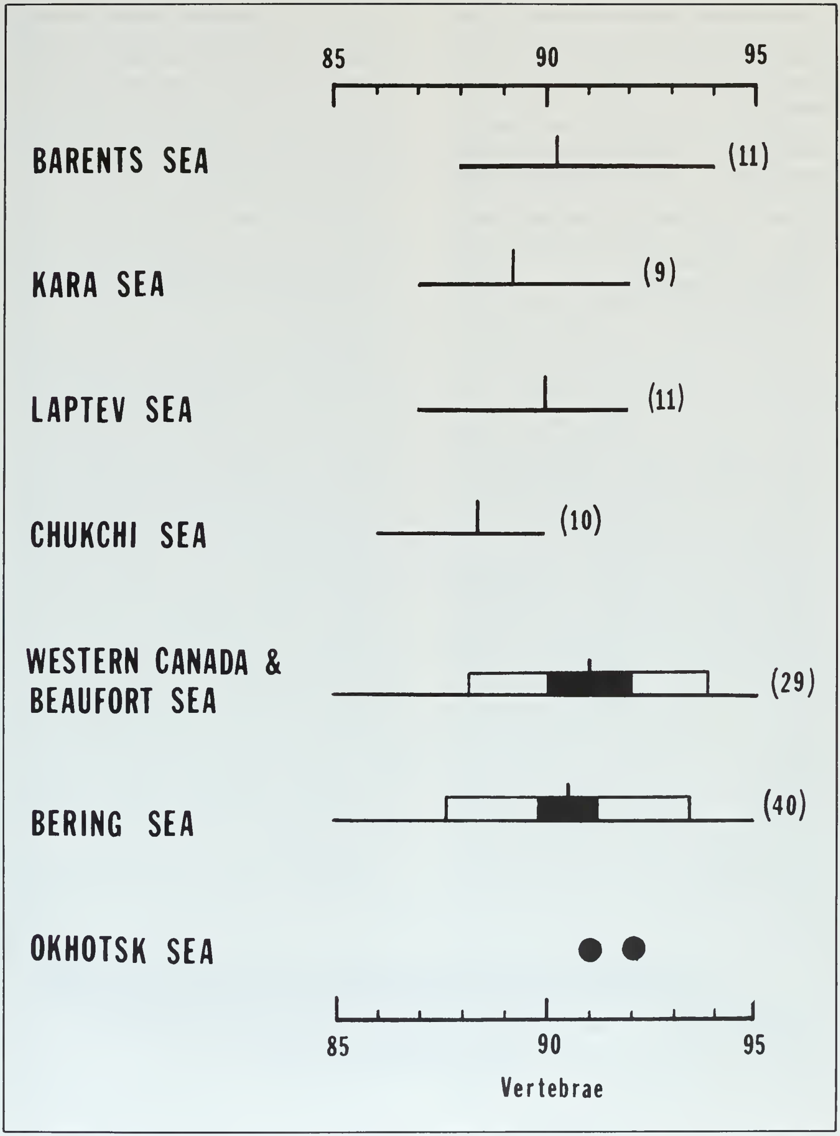

Figure 26. Geographic variation in total number of vertebrae in *Gymnelus hemifasciatus*. Sample sizes in parentheses; single dots represent one specimen. Graphics after Hubbs and Hubbs (1953).

Natural history. No reliable information exists on the biology of *G. hemifasciatus*. Food items noticed during this study include bivalves, polychaetes and gammarid amphipods, i.e., epi- and infaunal invertebrates similar to those found or reported for other species. Females ripen for first spawning at about 70–80 mm SL and ripe, young adult females (71–93 mm SL) carried 8–18 eggs 2.5–4.0 mm in diameter; larger females (105–125 mm SL) carried 20–26 eggs 3.6–4.4 mm in diameter. Spawning appears to occur in late summer or early autumn.

Etymology. From the Greek ημι- (half) and Latin "fascia" (band, stripe) in reference to the colour pattern.

Gymnelus popovi (Taranets and Andriashev, 1935)
Figure 27

Gymnelis viridis (non Fabricius). Bean 1882: 244 (partim); Gilbert 1895: 455 (partim); Bean and Bean 1897: 248; Rutter 1899: 192; Jordan and Gilbert 1899: 485 (partim); Evermann and Goldsborough 1907: 288 (partim); Gratsianov 1907: 433 (partim); Hofsten 1919: 63, fig. 15 (partim); Soldatov and Lindberg 1930: 507 (partim); Wilimovsky 1954: 288 (partim); Wilimovsky 1964: 186.

Commandorella popovi Taranets and Andriashev 1935: 267–270, fig. 1 (original description); Andriashev 1937: 346; Taranets 1937: 165; Andriashev 1939a: 51; Andriashev 1954: 261; Quast and Hall 1972: 13; Fedorov 1973: 57.

Commanderella sp. Wilimovsky 1964: 186 (lapsus calami).

Remarks. In September, 1932, the USNM received nine zoarcid fishes from ZIL, including one specimen from ZIL 23948 (remaining specimen designated holotype of *Commandorella popovi*). This was followed by a manuscript by A.M. Popov reviewing the zoarcids of the Soviet Far-East which included description of ZIL 23948, but this was never published. Leonhardt Stejneger of the U.S. National Museum identified a specimen of Popov's with those he collected in 1882–1883 in the Commander Islands, but also never published. USNM 124968 and USNM 150564 were manuscript types of Charles H. Gilbert, dating from 1907.

Holotype. A female, 128 mm standard length (SL), ZIL 23948, Copper (Mednyy) Island, Commander Islands, western Bering Sea, 3 July 1911, intertidal zone; collected by E.K. Suvorov.

Paratype: ZIL 23950, Copper Island, 1910, E.K. Suvorov.

Diagnosis. *Gymnelus popovi* is distinguished from all other species in the genus by the following combination of characters: vertebrae 92–103 ($\bar{x}$ = 96.9, SD = 2.7, N = 85); dorsal fin rays 91–101; anal fin rays 72–80; pectoral B/L ratio 42–55% ($\bar{x}$ = 49.3%, N = 37) in fish over 80 mm SL; free dorsal fin pterygiophores 0–1; dorsal fin origin extending from vertical with pectoral fin base to vertical 15–20% pectoral fin length posterior to pectoral base; branchiostegal rays usually six; pectoral fin rays 10–13 (usually 11 or 12); vomerine and palatine teeth always absent; following cephalic lateralis pore counts are from fully developed fish (greater than about 60 mm SL): preoperculomandibular pores 7–8 (seven in only one fish); suborbital pores 5–7 (usually six); interorbital pore always present; postorbital pores 3–5 (usually four); occipital pores three; body and tail usually brown or red with irregular yellowish ventrum and characteristic dark reticulations on sides of head and body in younger fish; females mature at about 80–90 mm SL.

Description. Counts and measurements are given Table 2. Body elongate, never wider than

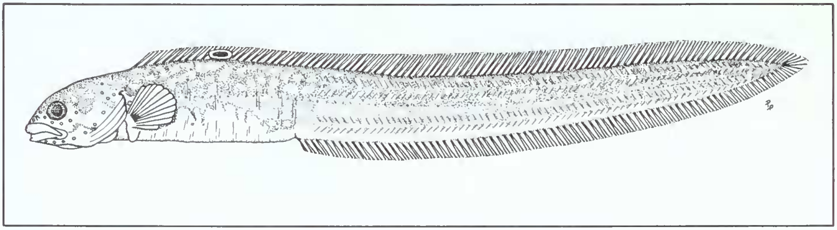

Figure 27. *Gymnelus popovi*: juvenile female, 88 mm SL, UWZ 3558, Umnak Island, Aleutian archipelago.

head. Head ovoid, dorsal profile when viewed laterally more acute in juveniles than adults; low snout ridge formed by frontal bones distinct, imparting characteristic rounded features to snout region. Eyes excluded from lateral profile of head when viewed dorsally in fish larger than about 90–95 mm SL. Head width not significantly wider in males than females, juveniles with narrower heads than adults. Head length (HL) longer in males than females (Fig. 17). A t-test for significance in difference of the ratio of HL to SL (arcsine transformed) for males versus females gave a value of 4.21, significant at $p<.001$ with 27 degrees of freedom. Eye diameter 18.5–29.9% HL, ratio subject to great individual variation. A linear regression of the ratio of eye diameter to head length versus head length gave a poor correlation coefficient ($r=-.434$, $N=33$). Body depth at anal fin origin 7.3–9.5% SL, ratio also poorly correlated with length ($r=-.525$, $N=26$). Mouth terminal, upper lip slightly overhanging lower in both adults and young juveniles; upper lip with free fold across snout; lower lip adnate to chin tip in all specimens examined, contrary to that reported by Andriashev (1937); with small fleshy fold anteriorly. Upper jaw length 46.0–54.4% HL ($\bar{x}$ = 41.0%) for 13 adult females. Teeth on jaws more inwardly recurved in juveniles than adults, no significant sexual differences in numbers of jaw teeth. Teeth on vomer and palatines always absent. Dorsoposteriormost edge of operculum with evenly rounded posteriorly directed flap in adults, more irregular in outine in juveniles. Gill slit more vertical in largest specimens, not extending anteriorly in some of these; usually extending to opposite fifth to seventh pectoral fin ray in most fish regardless of size, to opposite second to fourth ray in 11% of sample ($N=94$). Maximum number of gill rakers on upper limb develop by about 85–100 mm SL, by about 70–80 mm SL on lower limb. Outer gill rakers on lower limb overlap bases of adjacent rakers in fish over about 50 mm SL. Pseudobranchial filaments usually 5–7, eight in one fish. Branchiostegal rays six on one side, five on the other in two specimens; seven on one side, six on the other in one fish and six on both sides in all others (93 specimens). Lateral line with about 21–24 neuromasts anterior to vertical through anus. Dorsal branch of lateral line running to about one head length posterior to vertical with anus; composed of 15–17 neuromasts. Cephalic lateralis pore system usually complete. Preoperculomandibular pores usually eight (seven on one side, eight on the other in one fish 70 mm SL); pores develop by about 35–40 mm SL. Suborbital pores usually six (seven on both sides in two specimens; seven on one side, six on the other in one fish, five on both sides in one fish); pores open by about 45–50 mm SL. Postorbital pores usually four (three on one side, four on the other in one specimen; five on one side, four on the other in one specimen); pores develop by about 50–60 mm SL. Interorbital pore always present. Two anterior supraorbital pores in all fish examined (to 24 mm SL). Occipital pores three in all specimens examined over 26 mm SL.

Dorsal fin origin from above pectoral fin base to 15–20 percent pectoral fin length posterior to vertical with pectoral base. Dorsal origin associated with vertebrae 1–2; anal fin origin associated with vertebrae 20–24. One to five anal fin pterygiophores anterior to haemal spine of first caudal vertebra, none without associated fin ray. Zero or rarely, one free dorsal fin pterygiophore. Caudal fin with 1–2 rays associated with epural, 7–8 rays associated with hypural. Pectoral small, broadly rounded, rays not as exserted as other species, but ventralmost five or six rays most exserted; fin membrane thin, slightly thicker in adults than juveniles; usually 11–12 rays (Fig. 18). Precaudal vertebrae usually 20–23 (Fig. 19). Skin thicker than other *Gymnelus* of the same size, covering unpaired fins, scales absent. Maximum size to 163 mm SL.

Live colours reported from olive (light brown) to cherry red. Older specimens more monotone, especially dorsally, than younger ones. Youngest fish with fine dark reticular swathes or spots, dorsum darker than ventral surface of body or head. Characteristic reticular patterns behind eye separate darker dorsal area of head from light ventral surface (Fig. 27). In some fish this takes the form of a light bar extending from posterior margin of eye to preoperculomandibular canal. Ocelli black, ringed in white, when occurring. Ocelli appear in juveniles at about 45–55 mm SL and occurred in 43% of 88 fish examined over 55 mm SL. The sex ratio of fish with ocelli was 66% males, 34% females. Fish with ocelli usually had 1–3; only eight fish had 4–6 ocelli. Anal fin black in males over about 80–90 mm SL; females with light anal fin.

Distribution. Known from Kodiak Island, Alaska, westward across the Aleutian Islands to the Commander Islands, USSR. One collection from Shimushir Island in the Kurile archipelago (Fig. 28). Habitat rocky intertidal (lowest zones) in tidepools and channels. Associated chiefly with *Laminaria*, *Fucus*, *Ulva* and calcareous red algae or large boulders and gravel where algae is sparse. Depths recorded with captures range from above tidemark in wet seaweed at low tide to 2 m. Water temperatures recorded with captures range from about 6.0°C to 12.0°C. A description of a typical Aleutian Island intertidal habitat and associated fish fauna is found in Wilimovsky (1964). The present sample indicates a possible shift toward a greater number of vertebrae among western Pacific populations of *G. popovi*. However, this needs further testing when larger samples are available, particularly from the Commander and Kurile Islands (Fig. 29). Quast (1964) observed a similar east-west shift in number of unpaired fin rays and pored lateral line scales in the wide ranging hexagrammid fish *Hexagrammos lagocephalus*.

Natural history. Prior to this report only Taranets and Andriashev's (1935) five specimens were known in the literature, consequently nothing is known of the biology of *G. popovi*. Females ripen for first spawning at about 80–90 mm SL and ripe, young adult females (79–93 mm SL) carried 33–44 eggs 1.3–2.3 mm in diameter; larger females (103–121 mm SL) carried

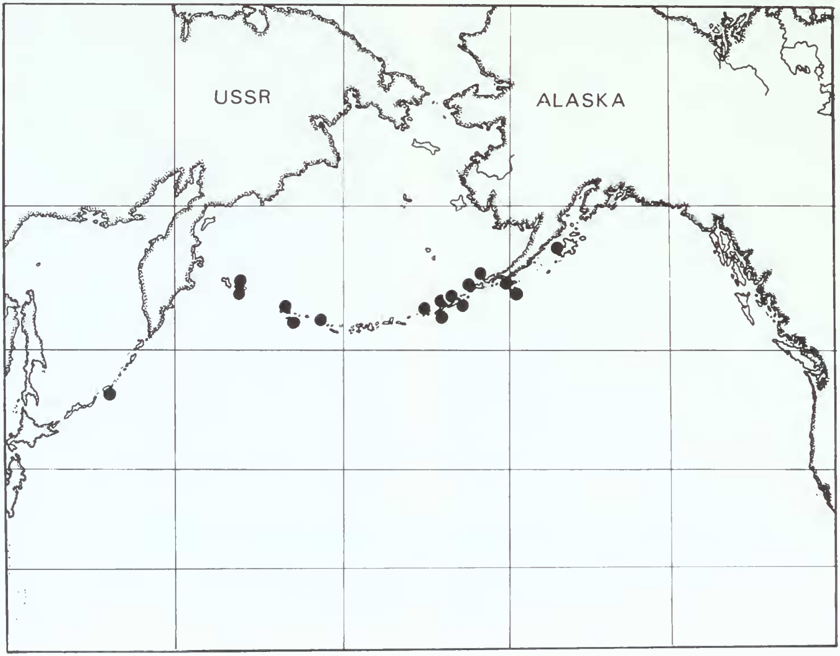

Figure 28. Distribution of *Gymnelus popovi*. One mark may represent more than one collection.

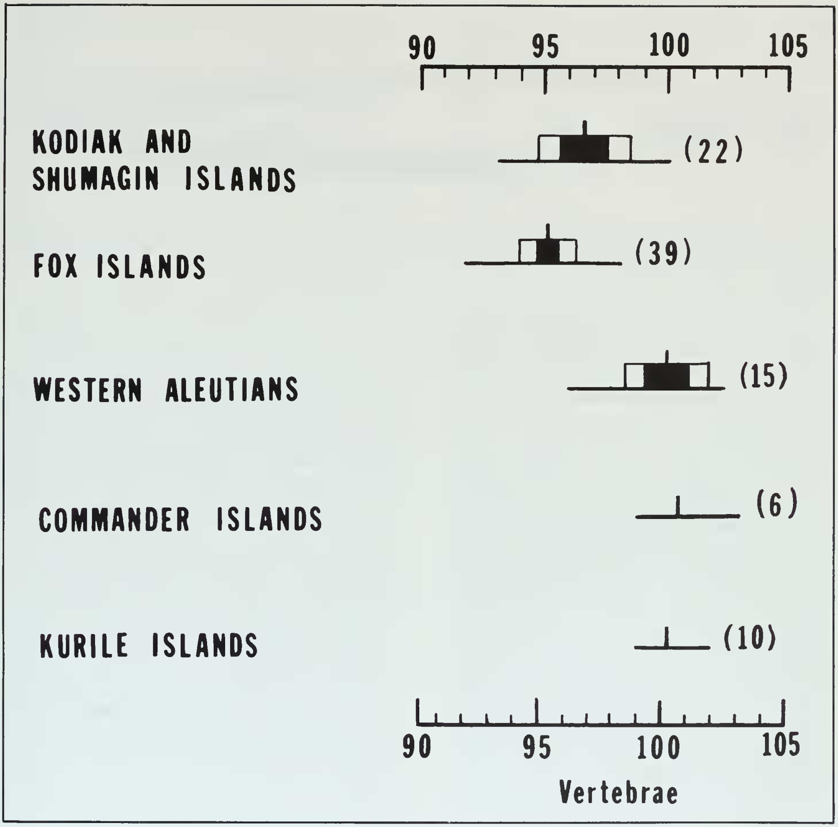

Figure 29. Geographic variation in total number of vertebrae in *Gymnelus popovi*. Sample sizes in parentheses. Graphics after Hubbs and Hubbs (1953). Western Aleutians refers to collections from Adak, Kiska, Agattu and Attu Islands.

45–52 eggs 1.9–2.4 mm in diameter. As in other species, the data suggest *G. popovi* spawns in late summer or early autumn, but there are no winter captures of large adults to date. I found polychaete and amphipod remains in stomachs of *G. popovi* and the species, like its congeners, probably preys exclusively on small epifaunal and, perhaps, infaunal invertebrates.

Etymology. Named in honor of A.M. Popov, ichthyologist of the Hydrobiological Laboratory of Leningrad State University and the Zoological Institute of the Academy of Sciences, USSR, Leningrad.

Gymnelus pauciporus n. sp.
Figures 12B, 30

Gymnelopsis ocellatus Soldatov. Shmidt 1950: tab. 26 (ZIL 23951; measurements).

Remarks. A.M. Popov recognized this species as undescribed and created a new genus for it, although these specimens were never described (Taranets, 1937). One specimen from ZIL 23945, one of Popov's manuscript types, was donated to

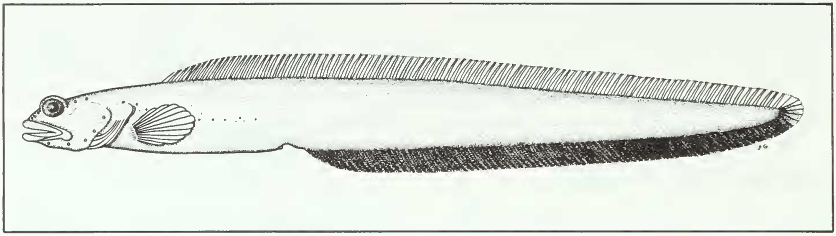

Figure 30. *Gymnelus pauciporus* n. sp.: holotype, adult male, 136 mm SL, USNM 92589, Kamchatka Coast.

USNM in 1932 and serves as holotype for the new species. It is unclear why Shmidt (1950) referred ZIL 23951 (1, 106 mm SL) to the scaled genus *Gymnelopsis*. The specimen I examined possessed all the diagnostic features of the new species and lacked scales.

Holotype. An adult male, 136 mm standard length (SL), USNM 92589, south of Cape Ozernoy, Kamchatka Peninsula, 57°31.0′N, 163°49.5′E, 275 m, 19 August 1920.

Paratypes. Two adult males, 131 and 132 mm SL, ZIL 23945, same data as holotype; ZIL 34498 (1 of 2), male, 119 mm SL, Ozernoy Bay, Kamchatka, 57°31.0′N, 163°17.5′E, ca. 40 m, 17 August 1920; ZIL 23951, male, 106 mm SL, Okhotsk Sea, R/V OKHOTSK, Sta. 11, 1913 (if same locality as 1912 Sta. 11, it would have same data as holotype of *Gymnelopsis brevifenestratus*).

Diagnosis. *Gymnelus pauciporus* is distinguished from all other species in the genus by the following combination of characters: vertebrae 88–93; dorsal fin rays 88–93; anal fin rays 70–74; pectoral B/L ratio 31–39%; no free dorsal fin pterygiophores; dorsal fin origin in front of vertical with middle of pectoral fin; branchiostegal rays 5–6; pectoral fin rays 11–12; vomerine and palatine teeth present; preoperculomandibular pores 5–6; suborbital, interorbital and occipital pores absent; postorbital pores 1–2.

Description. Counts and measurements are given in Table 2. This species is presently known from only five male specimens (type series). Body elongate, largest fish with greatly expanded cheeks, head wider than body in these. Head ovoid, dorsal profile when viewed laterally dorsoventrally flattened behind eye; snout evenly rounded in larger males, youngest fish with more acute snout. Eyes large, entering dorsal profile of head when viewed laterally; youngest male with eyes entering lateral profile of head when viewed dorsally. Head length 14.8–16.8% SL. Body depth at anal fin origin 7.2–8.6% SL, deepest in larger fish. Eye diameter 24.6–30.7% HL, larger in smallest fish. Mouth terminal, upper lip slightly overhanging lower; upper lip with free fold across snout; lower lip adnate to chin tip, anterior fleshy fold long, low. Upper jaw length 49.7–52.8% HL. Teeth on jaws small, conical, sharp. Teeth present on vomer, few (3-5), in roughly rounded patch. Teeth on palatines in a single row, with blunt tips. Dorsoposteriormost edge of gill slit slanting forward from vertical slightly, ventrally returning to more vertical inclination; tip forming somewhat angled, posteriorly directed flap meeting moderately developed skin fold on sides of body. Gill slit extending forward dorsally about 1/3 eye diameter; ventrally extending to opposite first to third pectoral fin ray. Gill rakers slender, thickest at bases, with pointed tips. Pseudobranchial filaments 6–8. Branchiostegal rays five on both sides in two fish, five on one side, six on the other in one fish, six on both sides in two. Lateral line traceable to just in front of vertical with anus in these old, faded specimens. Cephalic lateralis pore system greatly reduced (Fig. 12). Preoperculomandibular pores usually five, six in one fish. Suborbital, interorbital and occipital pores absent; no trace any started to form.

Dorsal fin origin associated with second vertebra. Dorsal fin rays equal to number of vertebrae except in one specimen which has one less fin ray. Anal fin origin associated with vertebrae 18–21. One to three anal fin pterygiophores anterior to haemal spine of first caudal vertebra, none without associated fin ray. No free dorsal fin pterygiophores. Caudal fin with two rays associated with epural, 8–9 rays associated with hypurals. Pectoral fin moderate, broadly rounded, ventralmost 5–7 rays slightly exserted; upper rays not exserted. Precaudal vertebrae 18–21. Skin moderately thick, covering unpaired fins in thin membrane. Maximum known size 136 mm SL.

Live colouration unknown. All specimens have faded in alcohol to a uniform light tan or gray. Dorsal fin lighter; anal fin in largest males dark brown, probably black in life.

Distribution. Known only from off Kamchatka Peninsula, Bering Sea and from one collection in the Okhotsk Sea (precise locality uncertain; Fig. 31). Reliable capture depths range from about 40 to 275 m.

Natural history. Unknown; apparently another upper slope-lower shelf dwelling species.

Etymology. From the Latin "paucus" (few) and "porus" (pore, passage) in reference to the reduced cephalic lateralis pore pattern; the name serves as a masculine noun in apposition.

Gymnelopsis Soldatov

Gymnelopsis Soldatov 1922: 160–161, fig. 1 (type species: *G. ocellatus* by original designation)
Derjuginia Popov 1931: 137–138, tab. 1, fig. 1 (type species: *D. ochotensis* by monotypy)
Gengea Katayama 1941: 591–593, fig. 1 (type species: *G. japonica* by original designation)

Description. Body elongate, subcircular in cross-section. Tail very long, laterally compressed, more so in juveniles than adults, tapering to blunt tip. Head subcircular in cross-section in juveniles, more dorsoventrally flattened in adults, males with large, well developed adductor mandibulae muscles; cheeks more or less parallel in juveniles. Eye circular, entering dorsal profile of head when viewed laterally in most fish, independent of age; eye diameter larger in percent of head length in younger fish. Upper jaw extending to about middle of eye in younger fish, to behind vertical through posterior margin of eye in adults; adult males with slightly longer jaws than females. Mouth terminal; upper lip slightly overhanging lower. Lips fleshy, upper with free fold across snout, lower adnate to chin tip. No submental crests or symphyseal knob formed. Teeth on jaws small, conical, in two or three rows in anterior patch on premaxillae, one or two rows anteriorly on dentary; no teeth on maxillae. Teeth on vomer and palatines in all specimens examined. Palatal and mandibular membranes well developed. Palate and floor of mouth with minute, scattered sensory papillae, crowded anteriorly. Gill rakers slender, roughly triangular, more acute in juveniles, without denticles. Gill arches four, space between all four; space restricted to lower half of last arch. Gill slit restricted, either entirely above pectoral fin base in most *G. brevifenestratus* and some *G. ochotensis*, or extending to opposite sixth pectoral fin ray. Gill slit slightly inclined anteroventrally except in *G. brevifenestratus* and *G. ochotensis* with slit above pectoral, in which case it is vertical. Opercular lobe usually continued forward at dorsal margin, meeting thickened skin fold on body to form siphon-like passage for water exiting branchial chamber.

Dorsal and anal fins long, low, confluent with caudal, their greatest height at fin's midpoint. Origin of dorsal fin either on vertical passing through pectoral fin base (*G. ocellatus*) or up to 1.2 head lengths behind pectoral base. Anal fin origin 0.8–1.4 head lengths behind pectoral base. Dorsal fin often embellished with ocelli in adults, independent of sex. Anal fin of males apparently black in all species except *G. ochotensis*. First dorsal fin ray a hard spine, remaining dorsal and all anal and caudal rays branched. Caudal fin rays 5–8; 1–2 rays associated with epural, 4–6 rays associated with hypurals. Pectoral fins small, rounded, with thin membranes, lower rays slightly exserted, with 9–12 rays. Pelvic fins and facial cirri absent. Scales present: cycloid, minute, imbedded in skin, not overlapping one another. Scales first appear on posterior portion of tail in young fish and develop in an anterior direction. Scales cover most of body and tail in *G. ochotensis*, absent on all fins; scales extend forward in a wedge-like pattern in other species up to a vertical through anterior fourth to half of anal fin length. Body lateral line mediolateral, incomplete, composed of free lateralis organs, without canal. Cephalic lateralis canals opening in small, rounded pores, with same canal systems as in *Gymnelus*. Pseudobranchial filaments well developed, about one eye diameter in length. Pyloric caeca two, blunt in adults, longer and finger-like in juveniles. Branchiostegal rays five except in *G. ocellatus*, which has six. Vertebrae amphicoelus and asymmetrical. Small, pointed genital papilla developed in adults of both sexes.

Etymology. From the Greek γυμνος (naked), ενχελος (eel) and οπσις (aspect, appearance)

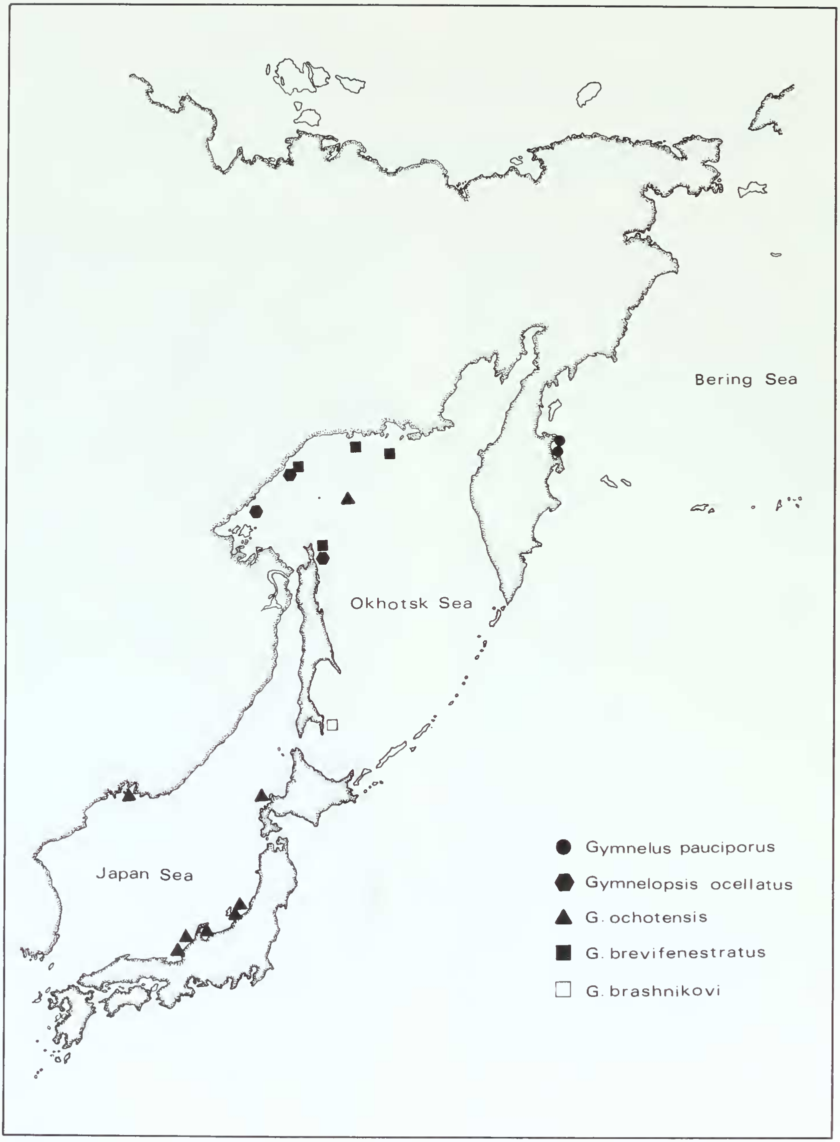

Figure 31. Distribution of *Gymnelus pauciporus* and all species of *Gymnelopsis*; specimens with accurate data only.

referring to its similarities with its scaleless relatives. Gender, masculine.

Gymnelopsis ochotensis (Popov, 1931)
Figures, 14A, 32

Derjuginia ochotensis Popov 1931: 137–138, tab. 1, fig. 1 (original description); Taranets 1937: 165; Shmidt 1950: 125–126, tab. 27; Matsubara 1955; 781; Norman 1966: 479; Ueno 1971: 86.
Gangea japonica Katayama 1941: 591–593, fig. 1; Katayama 1943: 101, 102, fig. 1; Matsubara 1955: 781; Mori 1956a: 22; Fowler 1958: 319; Honma 1963: 18; Takegawa and Morino 1970; 383; Shiino 1972: 129; Lindberg and Krasyukova 1975: 180, 181, fig. 143.

Holotype. A juvenile male, 108 mm standard length (SL), ZIL 30359, northern Okhotsk Sea, 56°08′N, 144°55′E, 1 August 1929, 287 m.

Paratype. None.

Diagnosis. *Gymnelopsis ochotensis* is distinguished from all other species in the genus by the following combination of characters: vertebrae 106–114; dorsal fin rays 90–103: anal fin rays 90–96; pectoral B/L ratio 36–46%; free dorsal fin pterygiophores 7–12; dorsal fin origin always behind vertical through posterior margin of pectoral fin; branchiostegal rays five; pectoral fin rays 10–11; vomerine and palatine teeth present; preoperculomandibular pores 5–6; suborbital pores 6–7; interorbital pore present; postorbital pores 3–4; occipital pores 1–3; large, irregular black blotch on pectoral fin; scales in adults develop on body from behind pectoral fin base to tail tip.

Description. Counts and measurements are given in Table 3. This species is presently known from only 10 specimens. Body elongate, head wider than body in adult males. Head ovoid, dorsal profile when viewed laterally more acute in adults than juveniles due to steeper snout caused by larger, more pronounced eyes in juveniles. Eyes large, ovoid, entering lateral profile of head when viewed dorsally. Head length 13.7–16.1% SL. Body depth at anal fin origin 6.0–7.6% SL, deepest in larger fish. Eye diameter 27.2–34.6% HL, smaller in diameter in largest fish. Preanal length slightly shorter than all other *Gymnelopsis* species: 29.6–34.1% SL. Mouth terminal, upper lip slightly overhanging lower; upper lip with free fold across snout; lower adnate to chin, anterior fleshy fold long, low, not prominent. Upper jaw length 36.8–54.3% HL, lower jaw length 34.2–51.6% HL (measured across lips to rictus). Shmidt (1950) reported a longer lower jaw than upper, but his method of measuring is unknown and for lower jaw may have extended from tip of chin to posterior edge of anguloarticular. Teeth on jaws moderate, recurved inwardly, blunter in adults than juveniles. Teeth present on vomer and palatine bones, relatively larger than other species. Dorsoposterior edge of operculum with angled, posteriorly directed flap, skin fold on body meeting this to form well developed siphon. Gill slit nearly vertical, extending forward above about one third eye diameter. Gill slit extending ventrally to opposite first to fourth pectoral ray in material studied, Shmidt (1950) reported gill opening ". . . descending to one-half and even one-fourth of the pectoral fin base." Pseudobranchial filaments 4–6. Branchiostegal rays five on both sides in all fish. Lateral line with 41–47 neuromasts in all; 20–23 anterior to vertical with anus. Dorsal branch of lateral line composed of 16–18 (?) neuromasts, extending to about half head length posterior to dorsal fin origin. Cephalic lateralis pore pattern relatively well developed (Fig. 14). Preoperculomandibular pores usually six, five in one specimen on both sides due to the failure of one pair of pores to develop. Suborbital pores usually six, seven on

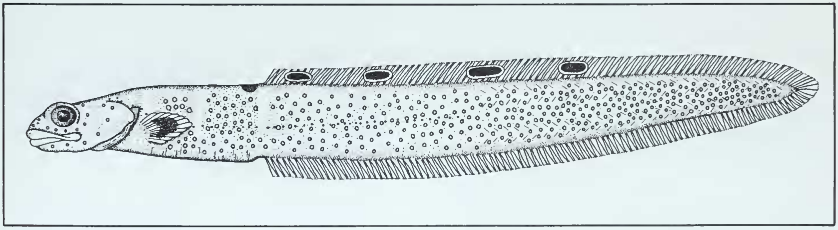

Figure 32. *Gymnelopsis ochotensis*: adult male, 223 mm SL, USNM 117958, Japan Sea.

one side in two fish. Postorbital pores usually three, four in only one fish (holotype). Interorbital pore present, set nearly on horizontal with posterior margin of eye; two anterior supraorbital pores. Occipital pores one or three, when one, only central pore developed. Dorsal fin origin associated with vertebrae 11–17; anal fin origin associated with vertebrae 17–19. One or two anal fin pterygiophores anterior to haemal spine of first caudal vertebra, none without associated fin ray. Seven to 12 free dorsal fin pterygiophores. Caudal fin with 1–2 rays associated with epural, 6–7 rays associated with hypurals. Pectoral fin with lowermost 5–6 rays slightly exserted. Precaudal vertebrae 18–19. Skin thick, scale cover more complete than other species, extending on body to near pectoral fin base; absent from nape, abdomen and dorsal and anal fin bases anteriorly; present on dorsal and anal fin bases posteriorly. Maximum size 252 mm SL.

Shmidt (1950) records live colours as, ". . . yellowish with a grayish dorsal side and a lighter belly. . . 8 bluish-white, narrow, transverse bands. . . of which the first was situated behind the gill opening and the rest under the dorsal fin and extending onto it. Dorsal fin with 7 black ocellate spots ringed in yellow. Anal fin white with a rose border. Pectoral fins yellow. . ." In the present material, although very faded, dorsal bands easily seen, in none of the largest males is the entire anal fin pigmented. The number of ocelli ranged from one to five in the specimens studied.

Distribution. Known from northern Okhotsk Sea southward to Peter the Great Bay and off Hyogo Prefecture, Honshu, in the Japan Sea (Fig. 31). Habitat mud and gravel bottoms of upper continental slope, possibly occuring in deep rock formations. Depths recorded with capture ranged from 147 to 783 m.

Natural history. Unknown. The only female examined was in poor condition and not close to spawning.

Etymology. Named after the Okhotsk Sea.

Gymnelopsis brevifenestratus n. sp.
Figure 33

Gymnelopsis ocellatus (non Soldatov). Shmidt 1950: 123, tab. 26 (ZIL 23952, 23953; measurements), 124, 125 (partim).

Remarks. A.M. Popov also recognized this species as distinct, but never published his discovery. One specimen was donated by Popov to USNM in 1932 and serves as holotype for the new species.

Holotype. A young adult female, 89 mm standard length (SL), USNM 92587, Okhotsk Sea, 57°50′N, 141°47′E, 146 m, 30 June 1912; coll. F. Derbek, Eastern Ocean Hydrographical Expedition, R/V OKHOTSK, Sta. 11.

Paratypes. ZIL 23944 (74 mm SL), same data as holotype; ZIL 23952 (98 mm SL), same data as holotype; ZIL 23953 (122 mm SL); Okhotsk Sea, 54°14′N, 143°45′E, ca. 200 m, 12 July 1918; ZIL 33334 (6; 74–95 mm SL), Okhotsk Sea, 58°50.0′N, 146°14.8′E, ca. 110 m, 20 July 1916; ZIL 33751 (102 mm SL, male), Okhotsk Sea, Vityaz' Sta. 60, 175 m, 29 August 1949; ZIL 34842 (117 mm SL), Okhotsk Sea, 58°41.5′N, 149°47.5′E, ca. 100 m, 8 August 1915.

Diagnosis. *Gymnelopsis brevifenestratus* is distinguished from all other species in the genus by the following combination of characters: total vertebrae 89–96; precaudal vertebrae 16–18; dorsal fin rays 80–88; anal fin rays 72–80; pectoral B/L ratio 28–44%; free dorsal fin pterygiophores 3–5; dorsal fin origin on or slightly behind vertical with posterior margin of pectoral fin; gill slit either entirely above pectoral fin base or extending posteriorly to opposite first or

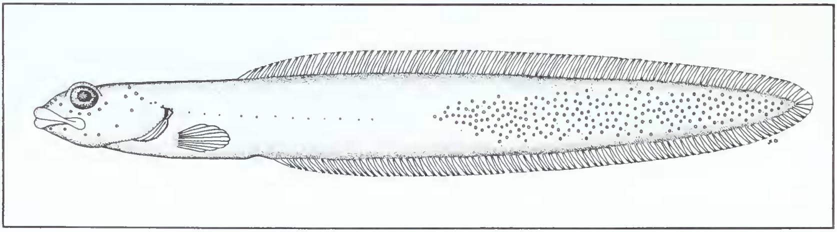

Figure 33. *Gymnelopsis brevifenestratus*: holotype, adult female, 89 mm SL, USNM 92587, Okhotsk Sea.

second pectoral fin ray; pectoral fin rays 9–11; vomerine and palatine teeth present; branchiostegal rays five; preoperculomandibular pores six; suborbital pores six; interorbital pore present; postorbital pores four; occipital pores three; scales develop to about one head length behind vertical with anal fin origin.

Description. Counts and measurements are given in Table 3. This species is currently known from only 13 late juveniles and adults. Body moderately elongate, compressed, head wider than body in largest males. Head ovoid, gently sloping behind eyes when viewed laterally; snout steeper in juveniles than adults. Eyes large, ovoid, entering dorsal profile of head when viewed laterally and lateral profile of head when viewed dorsally. Head length 14.3–16.8% SL. Body depth at anal fin origin 8.3–10.4% SL, deepest in largest fish. Eye diameter 27.5–37.7% HL, smaller in largest fish. Preanal length longest among *Gymnelopsis* (34.6–38.8% SL). Mouth terminal, upper lip very slightly overhanging lower; upper lip with free fold across snout; lower lip adnate to chin tip, anterior fleshy fold short, low, not prominent. Upper jaw in adult females extending to vertical with middle of eye or slightly behind; males with upper jaws extending behind vertical with posterior margin of eye; differences in jaw lengths not statistically detectable in such a small sample. Teeth on jaws longer and posteriorly sharper in adults than juveniles; recurved inwardly. Teeth present on vomer, rather numerous (7–10), in a roughly rounded patch. Palatine teeth in a single series, small, recurved inwardly. Gill slit vertical, above pectoral fin base or extending to opposite first, or on one side in one fish, second pectoral fin ray. Dorsoposteriormost edge of gill slit with small, angled flap meeting well developed skin fold on body to form siphon; gill slit extending anteriorly about one third eye diameter. Uppermost 3–4 gill rakers overlap bases of adjacent rakers and curve downwardly; lower rakers triangular. Pseudobranchial filaments four or five. Branchiostegal rays five on both sides in all fish. Lateral line traceable in present material to about one head length behind vertical through anus. Cephalic lateralis pores well developed. Preoperculomandibular pores six. Suborbital pores six. Postorbital pores four. Interorbital pore present, set posterior to vertical passing through pupils; two anterior supraorbital pores. Occipital pores three.

Dorsal fin origin associated with vertebrae 6–9, anal fin origin associated with vertebrae 16–18. Zero to two anal fin pterygiophores anterior to haemal spine of first caudal vertebra, none without fin ray. Three to five free dorsal fin pterygiophores. Caudal fin with 1–3 rays associated with epural, 5–6 rays associated with hypurals. Pectoral fin with lowermost 4–6 rays exserted, upper rays not exserted, but easily ripped free of membrane (condition in most fish). Precaudal vertebrae usually 16 or 17, 18 in two fish. Skin thick, fin membrane thin, delicate. Scales extending from about one to two head lengths behind anal fin origin to tail tip. Scales in smallest fish less numerous and more scattered than in adults. Maximum size to 122 mm SL.

Colouration in life unknown. All specimens have faded uniformly in alcohol. Whether males have dark anal fin is uncertain, but most likely they do.

Distribution. Known presently from only a few localities in the Okhotsk Sea (Fig. 31). Depths of capture indicate this is another lower shelf or upper slope species (about 100–200 m).

Natural history. Unknown. The holotype is a young adult female, 89 mm SL and contains about 25–30 eggs 1.8–1.9 mm in diameter.

Etymology. From the latin "brevis" (short) and "fenestra" (small opening, hole) in reference to the very small gill slit; the name serves as a masculine noun in apposition.

Gymnelopsis ocellatus Soldatov, 1922
Figures 14B, 34

Gymnelopsis ocellatus Soldatov 1922: 160, 161, fig. 1; Soldatov and Lindberg 1930: 504, 505, fig. 73; Taranets 1937: 165; Okada 1938: 260; Shmidt 1950: 124, 125, tab. 26 (partim); Matsubara 1955: 781; Norman 1966: 479; Lindberg and Krasyukova 1975; 178, fig 141.

Gymnelopsis ocellatus guntheri Shmidt 1950: 125, tab. 26.

Holotype. An immature male, 113 mm standard length (SL), ZIL 20167, western Okhotsk Sea, between Prokof'ev (Prokopiev) Island (Shantar Islands) and the village of Ayan, vic. 55°30'N, 138°30'E, ca. 70–90 m, 26 July 1912; coll. M.N. Pavlenko, R/V LEITENANT DYDYMOV, Sta. 168.

Paratype. None.

Diagnosis. *Gymnelopsis ocellatus* is distinguished from all other species in the genus by the following combination of characters: vertebrae 107–115; dorsal fin rays 109–114; anal fin rays 87–93; pectoral B/L ratio 28–36%; no free dorsal fin pterygiophores; dorsal fin origin in front of vertical with middle of pectoral fin; branchiostegal rays six; pectoral fin rays 10–12; vomerine and palatine teeth present; preoperculomandibular pores 6–7; suborbital and occipital pores absent; interorbital pore present; postorbital pores two; scales developed on posterior half of body.

Description. Counts and measurements are given in Table 3. This species is presently known from only six specimens (two males, one female, two undetermined). Body elongate, compressed laterally, head slightly wider than body in largest males. Head ovoid, dorsal profile when viewed laterally deepest at vertical with gill slit, evenly rounded to snout tip. Eyes moderate, ovoid, entering dorsal profile of head when viewed laterally, entering lateral profile when viewed dorsally. Head length 15.5–16.5% SL. Body depth at anal fin origin 6.1–10.3% SL, deepest in largest fish. Eye diameter 24.2–26.9% HL. Mouth terminal, lips equal; upper lip with free fold across snout; lower lip adnate to chin tip, anterior fleshy fold thick, high. Upper jaw length 44.0– 51.8% HL, extending behind posterior margin of eye in female. Teeth on jaws recurved inwardly; anterior teeth blunter than posterior teeth. Teeth present on vomer and palatine bones, with blunt tips; palatine teeth in a single series. Dorsoposteriormost edge of operculum evenly rounded, skin fold on body meeting this to form moderately developed siphon. Gill slit nearly vertical, barely slanting forward, extending anteriorly about 15–25% eye diameter. Gill slit extending ventrally to opposite third to sixth pectoral fin ray. Gill rakers thin, overlapping bases of adjacent rakers. Pseudobranchial filaments 4–5. Branchiostegal rays six on both sides in all specimens. Lateral line extending to about 1.5 head lengths posterior to anal fin origin. Cephalic lateralis pore pattern reduced (Fig. 14). Preoperculomandibular pores 6–7. Postorbital pores two. Interorbital pore present. Suborbital and occipital pores absent.

Dorsal fin origin associated with vertebrae 1–3, anal fin origin with vertebrae 21–23. Two to four anal fin pterygiophores anterior to haemal spine of first caudal vertebra, none without associated fin ray. No free dorsal fin pterygiophores. Caudal fin with 1–2 rays associated with epural, 4–6 rays associated with hypurals. Pectoral fin rays not discernibly exserted. Precaudal vertebrae 21–23. Skin thin, scale cover incomplete, extending as a wedge anteriorly, absent from unpaired fins. Maximum size 140 mm SL.

Colouration in life unknown, specimens all uniformly faded in alcohol to tan or brown. Fish possessed 3–5 ocelli in dorsal fin, which were black, surrounded by lighter ring, as in other species.

Distribution. Known only from the Okhotsk Sea in about 70–90 to 150 m (Fig. 31).

Natural history. Unknown; apparently a shelf-upper slope dwelling species.

Etymology. From the Latin "ocellus" (spotted as with eyes) in reference to the dorsal fin pigmentation in most specimens.

Gymnelopsis brashnikovi Soldatov, 1922

Gymnelopsis brashnikovi Soldatov 1922: 162 (no illustration); Soldatov and Lindberg 1930: 505; Taranets 1935: 98; Okada 1938: 260; Mori 1952: 130; Ki 1954: 349; Matsubara 1955: 782; Lindberg and Krasyukova 1975: 178–180, fig. 142.

Gymnelopsis ocellatus Soldatov. Taranets 1937: 14; Shmidt 1950: 123, tab. 26 (ZIL 13029), 124, 125 (partim).

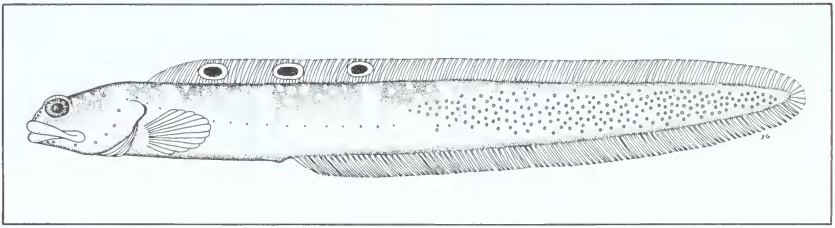

Figure 34. *Gymnelopsis ocellatus*: adult male, 134 mm SL, USNM 92588, Okhotsk Sea.

Remarks. Because species of *Gymnelopsis* are difficult to identify and the previous literature limited in scope and availability, records of this species in the southern Japan Sea (Mori, 1952; Ki, 1954) are considered tentative.

Holotype. A ripe female, 97 mm standard length (SL), ZIL 13029, southern Okhotsk Sea, off Cape Evstafiy (Eustaphie), southeast Sakhalin Island, vic. 46°15′N, 143°40′E, 79 m, 1899; coll. V.K. Brazhnikov.

Paratype. None.

Diagnosis. Only the holotype was available for study. *Gymnelopsis brashnikovi* is distinguished from all other species in the genus by the following combination of characters: vertebrae 111; dorsal fin rays 104; anal fin rays 90; four free dorsal fin pterygiophores; dorsal fin origin behind vertical through middle of pectoral fin; branchiostegal rays five; pectoral fin rays nine; vomer and palatine teeth present; preoperculomandibular pores seven; suborbital pores six; interorbital pore present; postorbital pores four; occipital pores three; scales extending from tail tip to about one head length behind anal fin origin.

Description. Counts and measurements of the holotype are given in Table 3. Body elongate, greatest depth between pectoral fin base and anus; body distended due to presence of large eggs in ovary. Head ovoid, cheeks parallel in dorsal view. Dorsal profile of head gently curved behind eyes, snout steep in lateral profile, also slightly curved. Eyes moderate, ovoid, entering dorsal profile of head when viewed laterally. Mouth terminal, upper lip with free fold across snout; lower lip adnate to chin, anterior free fleshy fold long, low. Teeth on jaws recurved inwardly, sharper posteriorly. Eight small, blunt teeth present on vomer in an irregular oval patch. Eight small teeth on each palatine bone, in a single row. Dorsoposterior edge of operculum with angled, posteriorly directed strut, weakly developed skin fold on body meeting this to form siphon. Gill slit steep vertically, extending forward dorsally less than 25% eye diameter. Gill slit extending ventrally to opposite second pectoral fin ray. Gill rakers on outer limb small, with pointed tips, overlapping bases of adjacent rakers. Pseudobranchial filaments four. Branchiostegal rays five on both sides. Lateral line not traceable posterior to anus in this faded specimen. Cephalic lateralis pore pattern relatively complete. Preoperculomandibular pores seven on both sides. Suborbital pores six on both sides. Postorbital pores four on both sides. Interorbital pore present; two anterior supraorbital pores, as in other species. Occipital pores three.

Dorsal fin origin associated with seventh precaudal vertebra (on vertical passing through ninth precaudal vertebra); anal fin origin associated with last precaudal vertebra (23rd). Three anal fin pterygiophores anterior to haemal spine of first caudal vertebra, all with fin rays. Four free dorsal fin pterygiophores. Caudal fin with one epural ray and six hypural rays. Pectoral fin with lowermost rays not noticeably more exserted than upper rays (membranes ripped in most places). Skin thin, faded, shriveled in alcohol. Scales reach to about two head lengths behind anal fin origin, anteriorly forming a wedge, as in *G. ocellatus*.

Colouration in life unknown, specimen now uniformly faded. Soldatov (1922) reported bars on the side of the body, but also reported this for *G. ocellatus* (no further colour notes given). Shmidt (1950) reported feeble traces of ocelli in the dorsal fin, these are not discernible today.

Distribution. Reliably known only from the type collection off Sakhalin Island, Okhotsk Sea. The records of Mori (1952) and Ki (1954) require verification.

Natural history. Unknown; holotype with 11 or 12 large eggs (2.8–3.1 mm in diameter). Collection date unknown.

Etymology. Named in honor of V.K. Brazhnikov, first Manager of Fisheries, Amur State Properties Board (1898), Khabarovsk, USSR.

Nemalycodes grigorjewi Herzenstein, 1896, nomen dubium

Herzenstein (1896) erected *Nemalycodes grigorjewi* for a single *Gymnelus* specimen (ZIL 9688) taken near the settlement Malyye Karmakuly, southwestern Novaya Zemlya in 1887. Knipovich (1901, 1908) placed *N. grigorjewi* in the synonymy of *Gymnelus viridis* and Andriashev (1954, 1973) supported that view. The small specimen (ca. 68 mm) is today very shriveled, brittle, greatly faded, eviscerated, broken in half and the tip of the tail is missing, thus reliable vertebral counts are impossible to obtain. A radiograph of the specimen reveals 18 + 73 (+) vertebrae and no free dorsal fin pterygiophores, thus it is not *G. retrodorsalis*. It may be a specimen of *G. viridis*, however, since Knipovich and Andriashev confused specimens of *G. hemifasciatus* with *G. viridis*, it also could be a specimen of *G. hemifasciatus*, which has also been taken off Malyye Karmakuly. Herzenstein's description is inadequate to differentiate his specimen and no illustration was published. Since it is impossible to positively identify ZIL 9688 and since it may be one of two species, I designate *Nemalycodes grigorjewi* nomen dubium.

Discussion

The species of *Gymnelus* and *Gymnelopsis* exhibit a confusing array of presumed pleisiomorphous (primitive) and apomorphous (derived) characters. For this reason, and chiefly because the general zoarcid character pool is virtually unknown, a phylogenetic reconstruction is not presented. For example, *Gymnelus hemifasciatus* and *G. pauciporus*, which have the lowest vertebral counts in the genus (assumed to be pleisiomorphous), possess a few reductional apomorphies thought to be correlated with life in deeper, outer shelf habitats: 1) reduced lateralis pore system (only to the occipital canal in *G. hemifasciatus*) and loss of tubular parietal channel of occipital canal in *G. hemifasciatus* (presumably also in *G. pauciporus*); 2) loss of ventral fork of posttemporal in *G. hemifasciatus* and 3) greatest tendency to lose the first pair of branchiostegal rays. It is unclear whether fewer vertebrae in these species is , in fact, a pleisiomorphous state or, alternatively, corresponds with general trends toward reduction of elements. Three species of *Gymnelopsis*, of the outer shelf-upper slope, have more vertebrae than any *Gymnelus*, suggesting that vertebral reduction accompanying adaptation to deeper water may not occur; that is, fewer vertebrae may indeed be pleisiomorphous. Deep-living *Lycodes* and *Lycenchelys* tend to have more vertebrae than their congeners living in shallower depths (Andriashev, 1954, 1955).

The loss of the first few dorsal fin rays, relatively high vertebral counts, more dorsoventrally constricted pectoral fin and high eastern Arctic distribution of *Gymnelus retrodorsalis* suggest it is one of the more derived species in the genus, probably a descendant of an earlier *G. viridis*-like ancestor. Like *G. retrodorsalis*, other eelpout species which have lost the first few dorsal fin rays usually inhabit greater depths than their congeners, viz. *Gymnelopsis ochotensis* and a few species of *Lycenchelys* (Andriashev, 1955).

A more complete cephalic lateralis pore system, anterior placement of the dorsal fin origin and smaller head seem to be pleisiomorphous characters retained by *Gymnelus popovi*, perhaps in response to its intertidal mode of life. These characters are shared with some intertidal stichaeids and Neozoarcinae (Makushok, 1958, 1961). The autapomorphous loss of vomerine and palatine teeth must in some way relate to feeding in *G. popovi*, but this is unclear.

A similar mixed group of apparently pleisiomorphous and apomorphous characters exist in *Gymnelopsis*. *G. ocellatus* possesses the most reduced cephalic lateralis pore system (apomorphy) but possesses no free dorsal fin pterygiophores and six branchiostegal rays (pleiosiomorphies). Among the other three species, which all have more complete lateralis pore systems, possess 3–12 free dorsal fin pterygiophores and all have five branchiostegal rays, *G. ochotensis* has a more complete scale cover (pleisiomorphy) than all other species. *Gymnelopsis brevifenestratus* has much fewer vertebrae (pleisiomorphy ?) than all other congeners. If fewer vertebrae is indeed primitive, it would appear that *G. brashnikovi* is derived from a *G. brevifenestratus*-like ancestor. The tendency toward reduction in size of the gill slit, as in *G. brevifenestratus* and *G. ochotensis*, has uncertain value at present, being observed in so few fish and being so variable in others.

Despite trends toward derived character states in *Gymnelopsis*, only its fewer caudal fin rays (5–8) are non-overlapping with any species of *Gymnelus* (with 9–12). These trends include: 1) more vertebrae (?), except in *Gymnelopsis brevifenestratus*; 2) more reduced preoperculomandibular pore pattern, except for *Gymnelus pauciporus*; 3) loss of first pair of branchiostegal rays, except in *Gymnelopsis ocellatus* and 4) more restricted gill slit, except in *G. ocellatus*. It is difficult to assess which is the more primitive genus. *Gymnelopsis* may not be as phyletically close to *Gymnelus* as to *Krusensterniella*, another scaled genus without pelvic fins, because of the following synapomorphies neither shares with *Gymnelus*: 1) five branchiostegal rays; 2) high vertebral counts (?; 115–119 in *Krusensterniella*); 3) reduced preoperculomandibular pore pattern (seven pores in *Krusensterniella*) and 4) reduced number of caudal fin rays (6–7 in *Krusensterniella*).

According to most recent theories, the Zoarcidae are thought to have originated and initially speciated throughout the North Pacific Ocean (Shmidt, 1950; Briggs, 1974; Peden and Anderson, 1978; Andriashev, pers. comm.). Shmidt (op. cit.) times the development of the major lineages of "cold-adapted" North Pacific teleost families (including Zoarcidae) with climatic deterioration during the Oligocene and Miocene. This is most profoundly described by a sudden drop in North Pacific bottom temperatures from about 4°C to 0°C in about two million years during the mid-Miocene (about 13–9 million years ago [Savin, 1977]). Unfortunately, no zoarcid fossils are known from this period. In fact, the only zoarcid fossils that seem to have been reported so far are Pliocene-Pleistocene otoliths of the Recent species *Lycodopsis pacifica* from California (Fitch, 1970, and others cited within; Zinsmeister, 1970). Despite this paucity of physical evidence, hypotheses surrounding the evolution of *Gymnelus* and *Gymnelopsis* may be posed if one accepts the reasonable *a priori* assumption of a North Pacific origin for the gymnelines.

When did the present species of *Gymnelus* become established in the Arctic Ocean? Herman and Hopkins (1980) reviewed the current paleoceanographic history of the Arctic and suggested that earlier hypotheses (summarized in Hopkins, 1967) that the Bering seaway opened for the first time in the Tertiary during the late Miocene (about 12–10 million years ago) were incorrect. The first Cenozoic Bering seaway apparently opened about 3.5 million years ago and then closed and reopened at least six, and perhaps as many as 10 times, between 3.5 million years ago and the present (Einarsson et al., 1967).

The repeated Pliocene-Pleistocene opening and closing of the Bering seaway must have been an important vicariant event for North Pacific and subsequent Arctic biotas; certainly it was to the dispersal of this fauna (diffusion, *sensu* Pielou, 1979:243). For example, the well known Pliocene Pacific-Atlantic faunal exchanges, best known in molluscs, echinoids and brachiopods (Durham and MacNeil, 1967) and fishes (Berg, 1918, 1934; Andriashev, 1939), reached their peak about 2–3 million years ago, characterizing the "youthful" Arctic marine ecosystem (Dunbar, 1968). But the lack of gymneline fossils and spatiotemporal uncertainty make biogeographic hypotheses difficult to test further than the idea that one or more *Gymnelus* populations entered the Arctic through any one or more of the Pliocene-Pleistocene seaways and subsequently possibly speciated and dispersed.

Pielou's (1978, 1979) quasi-sympatric model of speciation is an attractive one to help explain the origin of *Gymnelus popovi*, seemingly restricted to the rocky intertidal zone of the Aleutian-Kurile archipelagos and adjacent coastal shores. The fragmentation of a shallow water ancentral deme, one or more groups of which became adapted to intertidal life, could have become isolated in the islands during changes of sea level.

Shmidt (1950) believed the Okhotsk Sea served as a center of origin, not only for the North Pacific boreal fishes, but for most of the present Arctic groups as well. The sympatric ranges of all four *Gymnelopsis* species (and many other, larger genera such as *Lycodes*, *Careproctus* and *Liparis*) suggests dispersal into the Okhotsk Sea occurred repeatedly during the history of these genera. Also, because of more widespread climatic homogeneity in the entire North Pacific during the early Miocene (Frakes, 1979), Shmidt seems to have exaggerated the role of the Okhotsk Sea as an area of new species formation. Geographical events leading to possible allopatric speciation in the western North Pacific are obscure. Isolation of populations may relate to sea level changes with some populations having become extinct and others isolated as a result of local submergence or emergence, rather than to dispersal from a center of origin as favored by Shmidt (1950).

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Tables

Table 1. Diagnostic Characters of *Gymnelus* and *Gymnelopsis*

Character	*Gymnelus*	*Gymnelopsis*
Scales	Absent	Present
Caudal fin rays	9–12	5–8
Preoperculomandibular pores, adults	8*	5–7
Branchiostegal rays	6*	5, except in *G. ocellatus* (6)
Vertebrae	85–105	106–114, except in *G. brevifenestratus* (89–96)
Interorbital pore(s)	Absent, except in *G. popovi*	Present

* Except for a few, abberrant specimens.

Table 2. Counts and Measurements of *Gymnelus* Species

	Gymnelus viridis				*Gymnelus "bilabrus"*		*Gymnelus retrodorsalis*			
	N	R	$\bar{x}$	SD	N	R	N	R	$\bar{x}$	SD
Measurements as thousandths SL										
Predorsal length	69	153–208 (178)	181	10.7	3	183–208 (190)	62	183–363 (295)	298	9.8
Preanal length	69	351–392 (354)	370	6.7	3	362–392 (366)	40	339–420 (377)	378	9.0
Body depth	39	74–113 (90)	87	10.8	3	89–94 (93)	47	50–83 (78)	74	6.6
Head length	89	127–196 (154)	165	10.1	4	157–164 (169)	40	139–193 (161)	163	13.6
Head width	65	63–102 (69)**	81	10.9	3	84–110 (84)**	44	63–103 (79)**	81	10.9
Measurements as thousandths HL										
Length upper jaw	89	240–576 (427)**	422	52.7	4	431–555 (431)**	67	300–555 (513)**	440	50.3
Snout length	76	117–191 (175)	158	20.0	4	147–186 (181)	67	119–200 (152)	157	18.2
Eye diameter	86	201–359 (214)	263	10.0	4	231–257 (257)	66	252–422 (335)	324	33.8
Interorbital width	35	56–112 (73)	82	14.9	3	80–114 (80)	39	71–114 (86)	91	10.9
Length gill slit	61	206–311 (239)	258	26.4	3	275–295 (275)	54	184–358 (233)	260	30.6
Length pectoral base	67	207–303 (214)	261	21.9	3	217–261 (261)	64	135–209 (162)	173	12.7
Length pectoral fin	67	435–636 (449)	535	42.9	4	528–608 (576)	64	471–636 (528)	568	38.9
Pectoral B/L ratio, %	67	33–60 (48)	49	5.1	3	36–41 (45)	64	24–39 (30)	30	3.4
Counts										
Gill rakers	156	2–6+7–15=10–20(3+9)*	*	*	3	5+11=16(5+11)	64	2–5+7–11=10–15	*	*
No. free dorsal pterygiophores	181	0–2 (1)	*	*	4	0 (0)	79	3–14 (6)	*	*
Precaudal vertebrae	177	18–23 (20)	20.4	1.08	4	21–22 (21)	108	17–21 (19)	19.9	0.9
Caudal vertebrae	170	72–84 (82)	76.7	2.13	4	74–78 (76)	108	71–84 (79)	77.4	2.6
Total vertebrae	170	92–105 (102)	97.9	1.97	4	95–100 (97)	108	90–105 (98)	97.3	2.8
Dorsal fin rays	164	1,86–101 (1, 96)	95.6	2.04	4	1,92–96 (1,93)	69	1,76–97 (1,88)	89.0	4.2
Anal fin rays	161	72–84 (83)	77.2	2.19	4	76–79 (78)	69	72–85 (80)	77.6	2.7
Pectoral fin rays	170	10–14 (10)	12.3	0.48	4	12–13 (12)	86	9–12 (11)	10.3	0.6
Caudal fin rays	162	9–11 (10)	10.2	0.31	4	9–10 (9)	69	10–12 (10)	10.9	0.5
Vomerine teeth	96	0–12 (5)	*	*	4	5 (5)	77	0–11 (10)	*	*
Left palatine teeth	96	0–15 (10)	*	*	4	7–10 (7)	77	0–18 (8)	*	*
Branchiostegal rays	204	5–7 (6)	–	–	4	6 (6)	77	5–6 (6)	–	–
Pseudobranchial filaments	154	4–12 (7)	7.5	1.50	2	8–9 (9)	64	4–8 (–)	5.9	0.5
Suborbital pores	277	0–11 (6+8)	*	*	4	6–7 (7+6)	83	0–10 (7+7)	*	*
Preoperculomandibular pores	278	7–9 (8+8)	*	*	4	8 (8+8)	83	7–8 (8+8)	*	*
Anterior supraorbital pores	278	2–3 (2+2)	*	*	4	2 (2+2)	84	2 (2+2)	*	*
Interorbital pore(s)	277	0–1 (0)	*	*	4	0 (0)	84	0 (0)	*	*
Postorbital pores	276	0–5 (4+4)	*	*	4	4 (4)	84	0–6 (6+5)	*	*
Occipital pores	278	0–5 (2)	*	*	4	3 (3)	83	0–5 (2)	*	*
Standard length, mm	287	37–256 (147)	–	–	4	163–225 (163)	108	38–135 (122)	–	–

	Gymnelus hemifasciatus					*Gymnelus popovi*					*Gymnelus pauciporus*			
	N	R		$\bar{x}$	SD	N	R		$\bar{x}$	SD	N	R		$\bar{x}$
Measurements as thousandths SL														
Predorsal length	68	160–220	(164)	193	15.6	53	123–179	(149)	149	11.3	5	165–178	(172)	171
Preanal length	67	347–426	(360)	378	10.4	61	327–375	(—)	354	11.3	5	348–385	(348)	369
Body depth	45	74–106	(97)	87	7.9	69	73–95	(80)	81	5.8	5	72–80	(73)	79
Head length	82	148–187	(156)	167	19.4	57	115–185	(133)	146	13.1	5	148–168	(156)	157
Head width	45	60–114	(65)**	87	14.8	33	78–91	(63)**	82	8.0	5	81–97	(92)**	91
Measurements as thousandths HL														
Length upper jaw	86	333–623	(447)**	449	55.0	52	300–544	(481)**	420	57.4	4	497–528	(528)**	574
Snout length	78	118–228	(133)	157	18.1	42	114–199	(147)	158	22.6	4	142–171	(151)	157
Eye diameter	77	252–373	(347)	310	28.1	33	185–299	(259)	240	28.4	4	246–307	(259)	267
Interorbital width	77	77–122	(80)	101	13.3	65	84–122	(106)	98	8.9	4	76–93	(80)	82
Length gill slit	65	178–317	(206)	246	29.6	60	194–352	(—)	246	27.8	4	183–196	(193)	190
Length pectoral base	65	144–253	(207)	199	22.4	53	200–300	(265)	259	26.5	4	181–190	(193)	192
Length pectoral fin	64	466–610	(520)	543	34.9	53	406–563	(442)	513	34.9	4	498–631	(542)	549
Pectoral B/L ratio, %	64	26–46	(40)	36	6.0	53	42–55	(51)	49	4.0	4	31–39	(36)	35
Counts														
Gill rakers	72	3–6+7–11=9–15	(4+9)	*	*	77	2–5+7–11=10–16	(4+9)	*	*	4	4+8–10=12–14	(4+8)	*
No. free dorsal pterygiophores	80	0–2	(0)	*	*	85	0–1	(0)	*	*	5	0	(0)	–
Precaudal vertebrae	80	18–21	(18)	19.3	0.9	85	20–26	(23)	21.6	1.2	4	18–21	(21)	–
Caudal vertebrae	86	65–77	(73)	71.2	2.3	85	72–80	(76)	75.3	1.9	4	68–73	(72)	–
Total vertebrae	86	85–95	(91)	90.4	2.4	85	92–103	(99)	96.9	2.7	4	88–93	(93)	–
Dorsal fin rays	77	I,80–92	(I,85)	87.6	2.9	85	I,90–100	(I,97)	96.1	2.9	4	I,86–91	(I,91)	–
Anal fin rays	76	69–77	(75)	71.0	2.2	85	73–81	(73)	76.0	2.6	4	71–75	(75)	–
Pectoral fin rays	86	10–12	(12)	10.8	0.6	94	10–13	(13)	11.4	0.6	5	11–12	(11)	–
Caudal fin rays	76	9–10	(10)	9.4	0.4	85	9–10	(0)	9.5	0.4	3	10–11	(10)	–
Vomerine teeth	86	0–9	(6)	*	*	95	0	(0)	–	–	4	3–5	(3)	–
Left palatine teeth	85	0–14	(9+10)	*	*	95	0	(0)	–	–	4	5–8	(6)	–
Branchiostegal rays	88	5–7	(6)	–	–	96	5–7	(6)	–	–	5	5–6	(6)	–
Pseudobranchial filaments	60	4–8	(–)	5.4	0.8	78	5–8	(6)	5.5	0.6	2	6–8	(6)	–
Suborbital pores	84	0–9	(6)	*	*	93	1–7	(6)	*	*	5	0	(0)	–
Preoperculomandibular pores	84	4–8	(8)	*	*	93	6–8	(8)	*	*	5	5–6	(5)	–
Anterior supraorbital pores	84	2	(2)	*	*	93	2	(2)	*	*	5	2	(2)	–
Interorbital pore(s)	86	0–1	(4)	*	*	89	1–2	(1)	*	*	5	0	(0)	–
Postorbital pores	83	0–5	(2)	*	*	92	1–5	(4)	*	*	5	1–2	(2)	–
Occipital pores	82	0–3	(0)	*	*	93	0–3	(3)	*	*	5	0	(0)	–
Standard length, mm	113	28–140	(96)	–	–	97	24–163	(128)	–	–	5	106–136	(136)	–

(Holotypes or neotypes in parenthesis)
* Individual or age-dependent
** Sex related

(N) Sample size
(R) Range
($\bar{x}$) Mean
(SD) Standard deviation

Table 3. Counts and Measurements of *Gymnelopsis* Species

	Gymnelopsis ocellatus			*Gymnelopsis brashnikovi*	*Gymnelopsis brevifenestratus*			*Gymnelopsis ochotensis*		
	N	R	$\bar{x}$	Holotype	N	R	$\bar{x}$	N	R	$\bar{x}$
Measurements as thousandths SL										
Predorsal length	6	134–187 (187)	163	164	12	234–288 (259)	260	10	234–334 (234)	295
Preanal length	6	335–348 (341)	343	343	12	346–388 (355)	359	10	296–341 (314)	320
Body depth	6	61–103 (68)	82	84	13	83–104 (97)	92	10	60–76 (70)	68
Head length	6	155–165 (165)	160	142	13	143–168 (164)	157	10	137–161 (144)	147
Head width	6	56–89 (56)	71	57	12	62–98 (92)	78	10	54–94 (60)	68
Measurements as thousandths HL										
Length upper jaw	6	440–510 (440)	446	406	6	384–525 (390)	452	10	368–543 (368)	482
Snout length	6	154–215 (215)	181	181	6	158–198 (158)	173	10	135–179 (161)	160
Eye diameter	6	242–269 (242)	258	246	6	275–377 (336)	326	10	272–346 (329)	305
Interorbital width	6	63–78 (65)	71	87	6	63–89 (82)	72	10	64–104 (77)	75
Length gill slit	4	198–313 (198)	71	225	6	169–233 (171)	183	10	172–238 (238)	203
Length pectoral base	4	175–200 (177)	190	181	9	168–228 (185)	190	10	172–218 (206)	195
Length pectoral fin	5	558–634 (608)	591	565	9	490–583 (548)	566	10	433–516 (516)	480
Pectoral B/L ratio, %	5	28–36 (29)	32	32	9	28–44 (34)	36	10	36–46 (40)	41
Counts										
Gill rakers	6	2+8–10=10–12 (2+8)	*	3+9	4	2+7–8=9–10 (2+7)	*	10	3+9–11=12–14 (3+10)	*
No. free dorsal pterygiophores	6	0 (0)	*	4	13	3–5 (4)	*	10	7–12 (7)	*
Precaudal vertebrae	6	21–23 (21)	–	23	13	16–18 (16)	–	10	18–19 (18)	–
Caudal vertebrae	6	85–92 (89)	–	88	13	73–80 (76)	–	10	89–95 (94)	–
Total vertebrae	6	107–115 (110)	–	111	13	89–96 (92)	–	10	106–114 (112)	–
Dorsal fin rays	6	I,102–112 (I,105)	–	I,102	13	I,79–86 (I,81)	–	10	I,89–101 (I,101)	–
Anal fin rays	6	88–94 (92)	–	91	13	73–81 (78)	–	10	90–97 (96)	–
Pectoral fin rays	6	10–12 (11)	–	9	13	9–11 (11)	–	10	10–11 (11)	–
Caudal fin rays	6	5–7 (7)	–	7	8	6–8 (7)	–	10	7–8 (7)	–
Vomerine teeth	6	6–9 (6)	–	8	7	7–10 (8)	–	10	3–9 (8)	–
Left palatine teeth	6	9–13 (12)	–	8	8	5–9 (7)	–	10	5–12 (11)	–
Branchiostegal rays	6	6 (6)	–	5	8	5 (5)	–	10	5 (5)	–
Pseudobranchial filaments	6	4–5 (5)	–	4	4	4–5 (4)	–	10	4–6 (5)	–
Suborbital pores	6	0 (0)	–	6	4	6 (6)	–	10	6–7 (6)	–
Preoperculomandibular pores	6	6–7 (7)	–	7	4	6 (6)	–	10	5–6 (6)	–
Anterior supraorbital pores	6	2 (2)	–	2	4	2 (2)	–	10	2 (2)	–
Interorbital pore(s)	6	1 (1)	–	1	4	1 (1)	–	5	1 (1)	–
Postorbital pores	6	2 (2)	–	4	4	4 (4)	–	7	3–4 (4)	–
Occipital pores	6	0 (0)	–	3	4	3 (3)	–	10	1–3 (3)	–
Standard length, mm	6	82–140 (113)	–	97	13	74–120 (89)	–	10	108–252 (108)	–

(Holotypes in parenthesis; only holotype known of *G. brashnikovi*)
* Individual or age-dependent

(N) Sample size
(R) Range
($\bar{x}$) Mean

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Appendix I

Osteological abbreviations used in the text figures are listed below:
ACT – actinosts
AFP – anomalous fused pterygiophores
ANG – anguloarticular
BASBR 1–3 – first through third basibranchials
BASHY – basihyal
BOC – basioccipital
BrR – branchiostegal rays
CERBR 1–5 – first through fifth ceratobranchials
CERHY – ceratohyal
CL – cleithrum
COR – coracoid
DENT – dentary
DR – first dorsal fin ray
DS – dorsal fin spine
ECT – ectopterygoid
END – endopterygoid
EP – epural
EPIBR 1– –4 first through fourth epibranchials
EPIHY – epihyal
EPIO – epioccipital
EPLEU – epipleural rib
ETH CART – ethmoid cartilage
EXOC – exoccipital
FR – frontal
HYOM – hyomandibula
HYPBR 1–3 – first through third hypobranchials
HYPHY D – dorsal hypohyal
HYPHY V – ventral hypohyal
I2–4 + P – infrapharyngobranchials 2–4 plus fused tooth plates
INTHY – interhyal
IO – interorbital pore
IOP – interopercle
L EX – lateral extrascapular
LAC – lacrymal
LAT ETH – lateral ethmoid
MAX – maxilla
MES – mesethmoid
MET – metapterygoid
NAS – nasal bone
OCC – occipital pores
OP – opercle
PAL – palatine
PAR – parietal
PAS – parasphenoid
PCL – postcleithrum
PEL – pelvic bones
PLEU – pleural rib
PM – preoperculomandibular pores
PMAX – premaxilla
PO – postorbital pores
POP – preopercle
POSTZ H – haemal postzygapophysis
POSTZ N – neural postzygapophysis
PP – proximal pterygiophores
PREZ H – haemal prezygapophysis
PREZ N – neural prezygapophysis
PRO – prootic
PTEM – posttemporal
PTO – pterotic
PTS – pterosphenoid
PU 1+U 1+UR+H+PH – fused first preural centrum, ural centrum, uroneural, hypurals and parhypural
QUAD – quadrate
RET – retroarticular
SCAP – scapula
SO 1–6 – suborbital bones
SOC – supraoccipital
SOP – subopercle
SPH – sphenotic
SUB – suborbital pores
SUCL – supracleithrum
SUP – supraorbital pores
SYM – symplectic
TAR – terminal anal fin ray
TDR – terminal dorsal fin ray
UROHY – urohyal
V – vomer

Appendix II

Specimens examined in this study are listed below; all extant type material is listed in the accounts (except *Gengea japonica*, which was not located). Specimens for which data seems questionable or is substantially lacking are listed separately after each species' major listing. The number of specimens in each lot is listed in parentheses after the catalogue number.

Gymnelus viridis (Fabricius)

GREENLAND, no specific locality: ZIL 1945 (5); gift of MNHN; of Reinhardt, 1842. BMNH 1846.2.16.24 (1). BMNH 1846.2.16.30 (1 of 2). BMNH 1846.2.16.38-39 (2). SU 9575 (1). USNM 39727 (1). USNM 39767 (1). USNM 39751 (1). USNM 39775 (1) (preceding 4 with labels indicative of Reinhardt's specimens; donated by Copenhagen Museum). USNM 28636 (1); N.P. Scudder, 1879. ZMUC 2-46 (45); of Reinhardt; of these, following with collection data: ZMUC P761098 (#44) (1), 24 Oct. 1829, Vahl; ZMUC P761099 (#45) (1), 24 Oct. 1829, Vahl; ZMUC 13 (1), 1 Sept. 1832, Möller; ZMUC 14 (1), 24 Oct. 1829, Vahl; ZMUC 23 (1), 3 Sept. 1833, Ager; ZMUC 16 (1), 22 Oct. 1832, Molgfeldt. GREENLAND, WITH LOCALITY DATA: Lindenowfjord, vic. 60°30′N, 43°50′W: ZMUC P76892 (1), 5-75 m, 30 Aug. 1932; ZMUC P76891 (1) (same data as preceding); ZMUC P76194 (1) and P76195 (1), 100-150 m, 28 July 1935. Nannortalik, vic. 60°08′N, 45°08′W: ZMUC P76180a-d (4), in kelp, 19 Sept. 1929; ZMUC 189 (1), coll. Lutzen. Julianehaab, vic. 61°00′N, 45°55′W: ZMUC 197 (1) and 198 (1), 16 Jan. 1901; ZMUC 199 (1), 24 Jan. 1893; ZMUC 200 (1), May 1902; ZMUC 201 (1), 9 Oct. 1906; ZMUC P76169 (1), 13 March 1899. Fyllas Banke, vic. 63°50′N, 52°45′W: ZMUC 48 (1), 146 m, 7 July 1884; ZMUC 49 (1), 20 Oct. 1884; ZMUC P76172 (1) and P76173 (1), 63°36′N, 52°34′W, 53 m, 6 July 1925. Godthab, vic. 64°10′N, 51°45′W: ZMUO 2992 and 2993, Bauman, 1892. Store Hellefiskebanke, vic. 66°30′N, 68°00′W to 59°00′N, 62°00′W: ZMUC 15xx (1), 16xx (1) and 17xx (1), 73 m, 16 Sept. 1886; ZMUC 209 (1) and 210 (1), Ingolf Exped. 1895-96; sta. 29 (65°34′N, 54°31′W, 124 m) and sta. 34 (65°17′N, 54°17′W, 101 m), specimens and data mixed. Egedesminde, vic. 68°40′N, 52°40′W: ZMUC 188 (1), coll. Olrick, July 1861. West of Disko Bay, 68°52.0′N, 55°46.5′W: FOCN 6647 (1), 101-110 m, 1 Aug. 1965. Cape York, vic. 75°50′N, 66°00′W: ZMUC P76170 (1), at tide mark, 9 Aug. 1914; ZMUC P76171 (1), coll. P. Freuchen, 1920. Wolstenholme Sound (Bylot Sound), vic. 76°30′N, 69°00′W: ZMUC P7687 (1), Freuchen, 15 Dec. 1919. Smith Sound: ZMUC P76177 (1), P76178 (1) and P76179 (1), 76°40′N, 76°20′W, 85 m, 16 Aug. 1928. Gaasefjord, vic. 70°10′N, 27°00′W: ZMUO 6634 (1), coll. Fridtjof Nansen, 30 Aug. 1901.

CANADA; Nova Scotia: NMC 65-308 (1): 44°58′N, 60°40′W, 183-201 m, 13 Aug. 1965. Newfoundland: USNM 45956 (1): 46°37.0′N, 49°50.5′W, 71 m, 25 Sept. 1885; FOCN 6018 (1): 46°21.0′N, 52°45.0′W, 165-168 m, 25 Jan. 1963; FOCN 2313 (1): Doctor's Ledge, Bonavista Bay, 37-91 m, 28 Aug. 1953; FOCN 7765 (1): Gulf of St. Lawrence, 49°36.0′N, 60°00.0′W, 113-119 m, 24 Jan. 1972. FOCN L8937 (1): 48°48.7′N, 59°24.7′W, 106-110 m, 3 June 1973. Quebec: NMC 70-6 (1): Saguenay Fjord, St. Lawrence River mouth, 48°25.5′N, 70°48.4′W, 12 m, 3 Aug. 1959; NMC 71-528 (1): Baie St. Catherine, St. Lawrence River mouth, 48°07′N, 69°43′W, 7 May 1934. Labrador: USNM 177574 (1): 55°04′N, 58°45′W, 7-13 m, 13 July 1952; USNM 177569 (1): 58°10′N, 62°50′W, 22 m, 20 July 1952; USNM 165291 (1): 53°30′N, 55°50′W, ca. 10-20 m, 28 Aug. 1952; FOCN 7726 (1): Hamilton Inlet Blk., 53°19.0′N, 53°53.5′N, 28 Oct. 1971; USNM 87659 (1), vic. Cape Mumford, coll. R.A. Bartlett, 19 Aug. 1925. Akpatok Island, Ungava Bay: NMC 60-449 (8), 60°25′N, 68°00′W, dropped by a murre, 10 Aug. 1954. Hudson Bay and Foxe Basin: USNM 94098 (1), 66°30′N, 80°00′W, ca. 50-60 m, 10 Aug. 1927; NMC 60-75 (1), 64°14′N, 76°32′W, 15 Sept. 1954; NMC 59-446 (1), 61°04.5′N, 69°39.0′W, 90-110 m, 21 July 1950; NMC 60-54 (1), off Mansel Isl., ca. 61°50′N, 78°40′W, 4 Aug. 1953; NMC 60-58 (1), 63°41′N, 80°12′W, 3 Sept. 1953; NMC 59-377A (1), 69°37.2′N, 81°06.3′W, 106 m, 1956; NMC 62-368 (1), 65°32.0′N, 84°52.0′W, 38-42 m, 25 Aug. 1961; NMC 62-302 (1), 69°21.5′N, 81°40.5′W, 2-18 m, 10 Oct. 1955; NMC 60-96 (1), 69°22.7′N, 81°44.2′W, 22-24 m, 2 July 1956; NMC 75-1893

(5), 61°58.0′N, 66°37.0′W, intertidal zone, 17 Aug. 1974; NMC 64-670 (1), 63°40.0′N, 87°20.0′W, 5 m, 6 Aug. 1961; USNM 94372 (1), Fury and Hecla Strait, 10-18 m, 3 Sept. 1933; USNM 94366 (1), Fury and Hecla Strait, 55 m, 3 Sept. 1933. Baffin Island, Perry Bay: NMC 76-287 (1), 61°58′N, 66°37′W, intertidal, 18 Aug. 1974; Frobisher Bay: USNM 121916 (1), 16.5 m, 5 Sept. 1942; NMC 70-280 (1), 63°15′N, 67°25′W, ca. 15-30 m, 8 Aug. 1970; NMC 70-281 (1), 63°41.8′N, 68°30′W, midwater trawl through *Laminaria* bed, 9 Aug. 1970; NMC 70-290 (1), 62°44′N, 65°35′W, 57 m, 20 Aug. 1970; NMC 77-1501B (3), 63°40′N, 65°35′W, 68 m, 11 Aug. 1970; NMC 77-1501C, same data as preceding; NMC 77-1501D, 62°50′N, 66°35′W, 256 m, 21 Aug. 1970; NMC 77-1501F (10), 62°41′N, 65°44′W, 92 m, 25 Aug. 1970; Cumberland Sound: USNM 21739 (2), coll. Ludwig Kumlien, 13 June 1878; USNM 21749 (4), Kumlien, 30 May 1878. BC 61-207 (1), 66°06′N, 65°58′W, ca. 20 m; Padloping Island: BC 61-219 (1), 67°03′N, 62°45′W, ca. 20 m, 18 Aug. 1953; Pond Inlet: BC 61-218 (1), 72°46′N, 77°00′W, ca. 30 m, 24 July 1955; Strathcona Sound: NMC 75-1943 (1), 73°10′N, 85°10′W, 75-80 m, 31 Aug. 1974; NMC 75-1948 (3), 73°10′N, 85°10′W, 2-5 m, 11 Aug. 1975. Devon Island: USNM 101104 (1), 75°40′N, 78°55′W, 13-18 m, 4 Aug. 1935; NMC 62-380 (1), 76°37.2′N, 96°21.6′W, 5 m, 14 July 1962. Coburg Island: USNM 88620 (1), vic. 77°30′N, 76°00′W. Ellesmere Island: ZMUO 6645 (1), vic. 76°20′N, 81°30′W, coll. Fritdjof Nansen, 12 July 1901; NMC 77-1094 (1), 82°24.0′N, 61°10.0′W, ca. 10-20 m, 9 July 1976; USNM 50231 (1), coll. R. Stein. Bellot Strait: NMC 76-126 (1), 72°00.6′N, 94°24.4′W, 3-12 m, 17 Aug. 1975. Boothia Peninsula: NMC 62-294 (1), 69°30.0′N, 93°30.4′W, 1959; Creswell Bay: NMC 62-531 (1), 72°45.2′N, 94°07.5′W, benthic grab in 9 m, 29 June 1962; NMC 76-0102 (1), 72°46′N, 93°41′W, intertidal, 2 Aug. 1975; NMC 65-349 (2), 72°46.3′N, 93°55.0′W, 11 m, 6 Aug. 1962; NMC 62-395 (2), 74°37.5′N, 94°26.2′W, 10 m, 25 July 1962; NMC 62-392 (1), 74°38.4′N, 94°16.8′W, 10 m, 17 July 1962; NMC 62-394 (4), 74°38.4′N, 94°17.2′W, 8 m, 25 July 1962; NMC 62-379 (5), 74°39.1′N, 94°15.7′W, 15 m, 13 July 1962; NMC 62-397 (3), 74°37.8′N, 94°13.0′W, 24 m, 25 July 1962; NMC 62-410 (3), 74°36.0′N, 94°13.0′W, 35-62 m, 6 Aug. 1962; NMC 62-399 (3), 74°38.4′N, 94°18.1′W, 6 m, 25 July 1962; NMC 62-406 (3), 74°38.3′N, 94°21.3′W, 4 m, 28 July 1962; NMC 62-408 (1), 74°37.5′N, 94°12.0′W, 10-30 m, 31 July 1962; NMC 65-355 (1), 74°37.5′N, 94°12.0′W, 10-30 m, 17 July 1962. Queen Maud Gulf: NMC 76-122 (1), 68°42′N, 100°23′W, 5-8 m, 13 Aug. 1975. Dease Strait: NMC 62-522 (1), 69°07′N, 105°10′W, 20 m, 10 Aug. 1962; NMC 62-419 (1), 69°10′N, 106°20′W, 20-30 m, 24 Aug. 1962. Franklin Bay: NMC 67-302 (7), 70°03.9′N, 125°28.5′W. ca. 100 m, 4 Aug. 1963; NMC 67-307 (1), 69°52.2′N, 125°49.0′W, ca. 50 m, 20 Aug. 1963. Liverpool Bay: NMC 75-168 (2), 69°35′N, 130°29′W, 8 m, 23 Aug. 1975; NMC 77-1260 (3), 69°48′N, 130°20′W, 8 m, 17 Aug. 1972; NMC 77-1224 (1), 69°25.6′N, 130°55.0′W, benthic grab in 18-22 m, 4 Aug. 1971; NMC 77-1252B (1), 69°47.2′N, 130°19.7′W, 6 m, 4 Sept. 1972; NMC 77-1261 (1), 69°48′N, 130°20′W, 5 m, 17 Aug. 1972; NMC 77-1205 (1), 69°34.7′N, 131°12.7′W, 3 m, 23 July 1971; NMC 77-1256 (2), 69°48′N, 130°20′W, 5-6 m, 17 Aug. 1972; NMC 77-1252A (1), 69°47.2′N, 130°19.6′W, 6 m, 4 Sept. 1972; NMC 77-1262 (3), 69°48′N, 130°20′W, 6 m, 17 Aug. 1972; NMC 77-1259 (7), same data as preceding.

ALASKA; Brownlow Pt.: NMC 74-276 (3), 70°34.8′N, 144°23.1′W, 71 m, 7 Aug. 1972. Macquarie Island: NMC 74-277 (2), 70°30.3′N, 144°21.6′W, 55 m, 7 Aug. 1972; NMC 74-284 (4), 70°35.1′N, 146°35.2′W, 48 m, 13 Aug. 1972. Point Barrow: USNM 152613 (1), vic. 71°40′N, 157°00′W, 66 m, 6 Aug. 1949; USNM 33948 (1), coll. J. Murdock, 13 Sept. 1882; BC 63-1141 (6), 71°21.5′N, 157°23.0′W, 19 Aug. 1954; BC 63-1225 (1), 71°23′N, 156°28′W, on beach, 28 Sept. 1950; SU 48809 (1), 70°51.5′N, 158°30′W, ca. 5-10 m, 10 Aug. 1954. Icy Cape: UA 1461 (1), 71°12′N, 163°05′W, 46 m, 29 Aug. 1973. Kotzebue Sound: UA 1423 (4 of 5), 68°16′N, 166°30′W, 18 m, 6 Sept. 1973; BC 61-76 (1), 67°43′N, 164°44′W, ca. 10-12 m, 9 Aug. 1959; BC 61-418 (1), 67°53.3′N, 166°43.0′W, ca. 28-30 m, 20 Aug. 1959; NMC 58-265 (1), 18 m, 10 July 1924. Bering Strait: UA 25931 (1), 65°29.5′N, 168°15.4′W, 57 m, 1 July 1977. St. Lawrence Island: BC 60-384 (2), 63°17′N, 169°28′W, intertidal zone, 3-4 July 1960. Nunivak Island: USNM 37035 (2), 60°N, 165°W, steamer CORWIN, 1884. Pribilof Islands: SU 3688 (1), 57°10.0′N, 170°47.3′W, 86 m, 3 Aug. 1891. Aleutian Islands: BCPM 980-569 (1), 53°03.6′N, 169°57.2′W, 146 m, 11 Aug. 1980.

USSR; Bering Sea: ZIL 25332 (2), Chukotsk Peninsula, 17 Oct. 1930; ZIL 34840 (1), Provideniya Bay, ca. 64°22′N, 173°20′W, intertidal zone, 16 July 1948; ZIL 35479 (1), tidepools in 2 m, 1 July 1955; ZIL 35423 (1), tidepools in 2 m, 3 July 1955. Cape Navarin: ZIL 34989 (3), Vityaz' sta. 582, 11 Sept. 1950; ZIL 34988 (1), Vityaz' sta. 567, 7 Sept. 1950. East Siberian Sea: ZIL 32756 (1), 71°17′N, 175°54′W, 42 m, 23 Aug. 1935; ZIL 32759 (3), 71°14′N, 177°12′W, 26 m, 17 Aug. 1935. Laptev Sea: ZIL 32764 (4), 76°59′N, 108°33′E, ca. 10-20 m, 29 Aug. 1913. ZIL 34984 (1), 75°17′N, 113°50′E, 43 m, 9 Sept. 1912. ZIL 14146 (1), 75°25′N, 137°30′E, 51 m, 28 July 1902. Barents Sea: ZIL 14157 (3), off Malyye Karmakuly, Novaya Zemlya, vic. 72°20′, 52°30′E, 9-14 m, 8 Aug. 1900. *Gymnelus viridis*. Specimens without data and questionable records: BMNH 1855.9.19.649 (1), Haslar Hospital Collection; BMNH 1855.9.19. 1298 (2), Haslar Hospital (syntypes of *Gymnelis pictus* Günther); BMNH 1852.8-9.12 (1), from Mr. Brandt; BMNH 1877.5.13.6 (1), Arctic Expedition, 1876; BMNH 1877.2.23-24 (2), same as preceding; BMNH, unreg., presented by Captain Sir James Ross, 72°N; MNHN 244.4.4.2 (var. *unimaculata*); MNHN 244.4.4.3; MNHN 244.4.4.4 (var. *trimaculata*) (preceding three with labels indicative of Reinhardt's material); BC 63-832 (1), coordinates given as 62°N, 154°W, (central Alaska), rock dredge, 4 Aug. 1953; USMN 117918 (1 of 9), Alaska, Attu Island in 247 m, 11 June 1906 (probable label switching); ZIL 31392 (1), 65°55′N, 169°09′E, (probably 179°09′W), 49 m, 14 August. 1932.

Gymnelus retrodorsalis Le Danois

CANADA; Newfoundland: NMC 63-156 (1), Bonavista Bay, ca. 48°45′N, 53°15′W, ca. 150-200 m, 2 June 1963. Baffin Island, Frobisher Bay: NMC 70-278 (1), 63°40′N, 68°26′W, 68 m, 7 Aug. 1979; NMC 70-280 (1), 63°40′N, 68°26′W, 59-68 m, 8 Aug. 1970; Strathcona Sound: NMC 75-1953 (1), 73°10′N, 85°10′W, 250-300 m, 31 Aug. 1975. Victoria Island, Dease Strait: NMC 77-1433 (1) 69°09.5′N, 105°52.7′W, 49-51 m, 17 Aug. 1966. Axel Heiberg Island: NMC 77-1092 (1), 80°24.5′N, 87°40.0′W, 8 m, 5 July 1976.

GREENLAND: Brønlund Fjord: ZMUC 70 (1), vic. 82°10′N, 31°30′W, 4 Aug. 1966. Danmarks Havn, vic. 76°50′N, 18°40′W: 15 ZMUC specimens, 1x, 2x, 4x-7x, 9x-17x. Davy Sound (King Oscar's Fjord): ZMUC P76190 (1), vic. 72°55′N, 24°55′W, 250 m, 25 Aug. 1932. Scoresby Sound: ZMUC P76174 (1), 10-18 m, 2 Sept. 1927; ZMUC P76175 (1), 8-14 m, 8 Sept. 1927; ZMUC P76176 (1), 12 m, 9 Sept. 1927. Hekla Havn (Danmarks Island), vic. 70°27′N, 26°12′W: ZMUC 194 (1), 5-9 m, 5 Apr. 1892; ZMUC 202 (1) and 203 (1), 5-11 m, 1891-1892. Henry Land, vic. 69°34′N, 23°35′W: ZMUC 204 (1), 37 m, 20 July 1900. Angmagssalik area, vic. 65°30-40′N, 37°30-40′W: ZMUC 192x (1), 16.5 m, 1900; ZMUC 193x (1), 28 Dec. 1902; ISH 782/64 (1), 62°30′N, 40°36′W, 200 m, 30 Mar. 1964; USNM 92304 (1), 37 m, 28 Aug. 1931. Lindenowfjord: ZMUC P76193 (1), vic. 60°30′N, 43°50′W, 125-150 m, 28 July 1935. Cape Farewell: ISH 61/55c (1), 59°41′N, 44°07′W, 140 m, 20 Sept. 1955; BMHN 1970.11.17.223-234 (12), 59°44′N, 45°10′W, 170 m, 11 Sept. 1952. Frederikshavn area: ISH 64/55b (1), 61°48′N, 50°27′W, 100 m, 23 Sept. 1955; ISH 65/55a (1), 62°38′N, 51°34′W, 100-150 m, 24 Sept. 1955; ISH 39/57 (1), 250 m, 15 Aug. 1957. Lille Hellefiskebanke: ISH 71/55b (1), 65°05′N, 54°24′W, 120 m, 28 Sept. 1955. Store Hellefiskebanke: ZMUC 208 (1), 211 (1) and 212 (1), sta. 29 (65°34′N, 54°31′W, 124 m) and sta. 34 (65°17′N, 54°17′W, 101 m) 1895-1896 Ingolf Expedition (specimens and locality data mixed); ZMUC 213 (1), 66°45′N, 56°23′W, 272 m, 20 May 1909; ZMUC 214 (1) and 215 (1), 66°44′N, 56°12′W, ca. 275 m, 20 May 1909; Godhavn: ZMUC P76191 (1), vic. 69°20′N, 53°30′W, 60-70 m, 13 July 1935. Baffin Bay, no specifics: ZMUC 18x (1), 19x (1) and 20x (1), 92 m, 16 Sept. 1886. Wolstenholme Sound (Bylot Sound): ZMUC Jrn. 31.12.1968 (1), 76°32′N, 69°19.9′W, 185 m, 20 Aug. 1968; Greenland, no specifics: BMNH 1846.2.16.30 (1 of 2).

DENMARK STRAIT: BMNH 1972.2.22.98 (1), 65°37′N, 29°35′W, 430 m.

JAN MAYEN: ZMUO 4985 (1), 70°41′N, 10°10′W, 481 m, 3 Aug. 1877.

BARENTS SEA; Svalbard (Spitsbergen): ZMUO 4983 (1), vic. 78°10′N, 15°00′E, coll. M. Sars, 27 July 1901; ZMUO 4984 (1), 79°51′N, 11°45′E, 15 Aug. 1878. South of Svalbard: BMNH 1970.11.17.222 (1), 76°10′N, 26°24′E, 141 m, 6 Sept. 1951; BMNH 1970.11.17.219 (1), 76°53′N, 13°38′E, 93 m, 30 Oct. 1951; BMNH 1965.6.22. 93-96 (4), 76°18′N, 17.00′E, 220 m, 11 Sept. 1951; BMNH 1965.6.22.97 (1), 74°54′N, 31°53′E, 285 m, 18 May 1957; BMNH 1965.6.22.98 (1), 74°40′N, 26°05′E, 311-339 m, 22 May 1953;

BMNH 1965.6.22.99 (1), 74°48′N, 28°33′E, 359 m, 22 May 1953; BMNH 1970.11.17.220 (1), 74°17′N, 23°20′E, 212 m, 24 June 1951; BMNH 1970.11.17.221 (1), 73°51′N, 20°14′E, 329 m, 8 Feb. 1951; ZIL 14137 (1), 71°58′N, 37°24′E, 293-298 m, 20 July 1899; ZIL 14138 (5), 72°47′N, 32°15′E, 280 m, 26 June 1899; ZIL 14140 (1), 75°00′N, 33°30′E, 213 m, 17 Aug. 1900. Novaya Zemlya vicinity: ZIL 32768 (3), Murmansk Expedition sta. 695, 1927; ZIL 14139 (3), 76°28.5′N, 57°03.0′E, 66 m, 30 July 1901; ZIL 14199 (1), same data as preceding; ZIL 14144 (1), 75°57′N, 50°54′E, 300 m, 12 Aug. 1901; ZIL 14155 (2), 76°28′N, 59°10′E, 118 m, 11 Aug. 1902; ZIL 14156 (5), 75°07′N, 54°51′E, 181 m, 10 Aug. 1902; ZIL 14159 (2), 76°30′N, 59°24′E, 194 m, 31 July 1901; ZIL 14160 (3), 77°31′N, 64°34′E, 280 m, 4 Aug. 1901.

KARA SEA: BMNH 1970.2.12.7 (1), 77°13′N, 96°04′E, 92 m, 25 Sept. 1933; ZIL 14148 (1), 76°08′N, 93°50′E, 275 m, 22 Sept. 1900; ZIL 29458 (1), 79°03′N, 85°48′E, 56 m, 3 Aug. 1934; ZIL 29453 (3), 78°06′N, 74°21′E, 387 m, 28 Aug. 1934; ZIL 29454 (2), 76°48′N, 93°40′E, 60 m, 28 Aug. 1933; ZIL 29455 (1), 75°59′N, 91°08′E, 55 m, 28 Aug. 1933; ZIL 29452 (5), 77°13′N, 96°04′E, 92 m, 25 Sept. 1933; ZIL 30531 (1), 81°11.2′N, 75°20.0′E, 124 m, 5 Sept. 1935; ZIL 30533 (1), 77°16′N, 96°54′E, 75 m, 11 Aug. 1937; ZIL 30558 (2), 78°52.8′N, 84°34.5′E, 40 m, 7 Aug. 1934; ZIL 32770 (1), 79°15.4′N, 100°04.0′E, 145 m, 20 Aug. 1932; ZIL 32074 (2), 79°18′N, 100°21′E, 400-300 m, 20 Aug. 1932.

Gymnelus hemifasciatus Andriashev

USSR: Barents Sea: ZIL 8513 (1), Novaya Zemlya, 1883; ZIL 14142 (1) 76°28′N, 59°10′E, 118 m, 11 Aug. 1902; ZIL 14143 (1), Kazinov Bay, Novaya Zemlya, vic. 71°N, 53°E, 9-17.5 m, 18 Aug. 1901; ZIL 14150 (1), 69°53′N, 43°30′E, 104 m, 7 Aug. 1900; ZIL 14153 (1), 72°29′N, 51°20′E, 73-74 m, 19 July 1901; ZIL 14154 (2), 74°02′N, 52°36′E, 154 m, 10 July 1902; ZIL 34106 (1), 70°30′N, 52°12′E, 102 m, 14 Sept. 1906; ZIL 35641 (3), 69°50′N, 51°43′N, 87 m, 15 Aug. 1957. Kara Sea: ZIL 29459 (1), 77°06.9′N, 87°50.0′E, ca. 40 m, 5 Sept. 1934; ZIL 29457 (1), 77°29′N, 83°50′E, 57 m, 3 Sept. 1934; ZIL 30682 (1), 76°48′N, 93°40′E, 60 m, 28 Aug. 1933; ZIL 32755 (1), 77°53′N, 79°45′E, ca. 80 m, 20 Aug. 1930; ZIL 32762 (1), 71°54′N, 67°45′E, 40 m, 9 Aug. 1931; ZIL 33941 (1) VNIRO Kara Exped., 9 m, 18 Sept. 1946; ZIL 34138 (2), Osetr sta. 2, 2 Sept. 1946. Laptev Sea: ZIL 14147 (2), 75°42′N, 124°42′E, 51 m, 6 Sept. 1901; ZIL 14161 (2), 75°38′N, 114°11′E, 19 m, 4 Sept. 1901; ZIL 23943 (2 of 3), 75°17′N, 113°50′E, ca. 10-20 m; USNM 92586 (1), same data as preceding; ZIL 30532 (1), 77°25.5′N, 115°45.2′E, 62 m, 1937; ZIL 30534 (1), 76°13.3′N, 129°45′E, ca. 60 m, 20 Aug. 1932; ZIL 30643 (1), 75°59′N, 117°10.4′E, ca. 30 m, 24 Aug. 1939; ZIL 32761 (1), Cape Chelyuskin, vic. 77°42′N, 104°20′E, intertidal zone, 30 Sept. 1932. East Siberian Sea: ZIL 32760 (1), 70°56′N, 175°35′E, 59 m, 11 Aug. 1929; ZIL 32758 (1), 72°30′N, 177°15′W, 61 m, 8 Sept. 1935; ZIL 32766 (1), 77°44′N, 145°32′E, ca. 50 m, 23 Aug. 1937. Chukchi Sea: ZIL 32757 (1), 69°54′N, 171°09′W, 45 m, 15 Sept. 1935. Bering Sea: ZIL 25241 (1), 64°27′N, 175°18′W, 69 m, 1 Aug. 1933; ZIL 30604 (1), same data as preceding; ZIL 25243 (1), Bering Island, ca. 55°N, 167°E, 123 m, 24 July 1929; ZIL 34438 (2), 57°31′N, 163°17.5′E, 54 m, 17 Aug. 1920; ZIL 34986 (3), Vityaz' sta. 596, 72 m, 15 Sept. 1950; ZIL 33938 (3), Anadyr Gulf, Vityaz' sta. 1527, ca. 80 m, 15 June 1952; ZIL 34983 (13), Anadyr Gulf, Vityaz' sta. 1007, 88-89 m, 11 Oct. 1951; BMNH 1970.2.12.6 (1), 57°31′N, 163°18′E, ca. 50 m, 19 Aug. 1920 (formerly ZIL 34987); ZIL 34751 (1), Vityaz' sta. 574, benthic grab, 8 Sept. 1950; ZIL 34832 (1), Vityaz' sta. 574, 8 Sept. 1950; ZIL 34860 (2), Vityaz' sta. 556, 80 m, 1 Sept. 1950; ZIL 34982 (1), Vityaz' sta. 558, 98 m, 1 Sept. 1950; ZIL 34990 (1), Vityaz' sta. 1357, Kronotskiy Gulf, Kamchatka, 180-200 m, 21 May 1952, ZIL 34999 (1), Vityaz' sta. 699/70, near Cape Lopatka, Kamchatka, 110 m, 18 April 1951. Okhotsk Sea: ZIL 20165 (1), between Prokof'ev Island and Ayan, ca. 55°30′N, 138°30′E, ca. 70-90 m, 26 July 1912; ZIL 20166 (2), Tauiskaya Bay, ca. 59°N, 150°E, 10 Aug. 1909; ZIL 25242 (1), Tauiskaya Bay, 18 Aug. 1930.

ALASKA; Gulf of Alaska: USNM 126717 (1), off Karluk, Kodiak Island, ca. 57°45′N, 154°35′W, Grampus sta. 601, from cod stomach, 27 July 1894; USNM 53874 (1), 58°05′N, 150°46′W, 93 m, 22 Aug. 1888. Bering Sea: USNM 59377 (1), 57°04.3′N, 170°52.5′W, 93 m, 3 Aug. 1891; USNM 48697 (1), same data as preceding; USNM 53875 (1), 57°31′N, 170°57′W, 90 m, 5 Aug. 1893; SU 3065 (1), 56°18.0′N, 164°34.1′W, 90 m, 14 June 1890; UW 8116 (1), off St. Lawrence Island, "Deep Sea 9," 26 June 1949; BC 63-1201 (1), 63°06′N, 171°42′W, ca. 50 m, 8 Aug. 1949;

BC 63-1203 (1), 64°27′N, 165°40′W, ca. 25 m, 14 Aug. 1949; BC 63-1209 (1), 64°44′N, 168°31′W, ca. 45 m, 24 Aug. 1949; BC 63-1205 (1), 65°07′N, 167°40′W, ca. 20-30 m, 15 Aug. 1949; BC 63-1202 (1), 64°30′N, 169°50′W, 55 m, 13 Aug. 1949; UA 1423 (1 of 5), 68°16′N, 166°30′W, 18 m, 6 Sept. 1973. Chukchi Sea: UA 1475 (1), 71°12′N, 163°05′W, 46 m, 29 Aug. 1973; UA 1224 (2), same data as preceding, 28 Aug. 1973; UA 1225 (1 of 5), 71°12′N, 164°12′W, 46 m, 28 Aug. 1973; UA 1190 (1), 71°23′N, 160°15′W, 46 m, 31 Aug. 1973. Beaufort Sea: SU 24668 (1), Pt. Barrow, coll. C.D. Brower; off Macquarie Island: NMC 74-284 (2), 70°35.1′N, 146°35.3′W, 48 m, 13 Aug. 1972: NMC 74-290 (2), 71°05.7′N, 148°41.0′W, 55 m, 19 Aug. 1972; off Brownlow Pt.: NMC 74-276 (6), 70°34.8′N, 144°23.1′W, 71 m, 7 Aug. 1972; NMC 74-281 (1), 70°33′N, 145°40′W, 50 m, 9 Aug. 1972.

CANADA: Liverpool Bay: NMC 75-164 (1), 69°49′N, 130°09′W, 73 m, 19 Aug. 1972; NMC 77-1258 (1), 69°48′N, 130°20′W, 6 m, 17 Aug. 1972; NMC 77-1248 (1), 69°41.1′N, 130°24.1′W, 11 m, 9 Aug. 1971; NMC 77-1267 (1), 69°50.5′N, 130°11.0′W, 6 m, 18 Aug. 1972; NMC 77-1255 (1), 69°48′N, 130°20′W, 6 m, 16 Aug. 1972; NMC 77-1214 (2), 69°46.5′N, 130°19.0′W, 10 m, 30 July 1971; NMC 77-1247 (2), 69°41.4′N, 130°28.1′W, 9 m, 9 Aug. 1971; NMC 77-1263 (1), 69°44.6′N, 130°18.0′W, 9 m, 16 Aug. 1972. Dease Strait: NMC 77-1428 (1), 69°09.5′N, 105°52.7′W, 53 m, 16 Aug. 1966; NMC 1367 (1), 69°09.5′N, 105°52.8′W, 53 m, 4 Aug. 1966; NMC 77-1370 (1), same data as preceding, 5 Aug. 1966; NMC 77-1402 (1), same data as preceding, 12 Aug. 1966.

Gymnelus hemifasciatus. Specimens without data and questionable records: ZIL 25240 (1), 57°07′N, 169°12′E (possibly 164°12′E?), 20 Aug. 1920; ZIL 32077 (2), Exped. A-60 (C-3), sta. 47, 132 m, 22 July 1948 (Arctic Ocean?); ZMUC 47 (1), no data, Dijmphna Exped., 1882, 84 m.

Gymnelus popovi (Taranets and Andriashev)

ALASKA; Kodiak Island, Karluk; vic. 57°40′N, 154°35′W: SU 5974 (11), shore coll., C. Rutter, May 1897; SU 7922 (there are 5 specimens bearing this number that seem to have come from SU 5974; catalogue entry reads, "West of Spitsbergen, 79°20′N, 10°10′E, 100 m, Zool. Polar Exped., 1900, Nordenskiöld." Specimens apparently mixed during 1906 earthquake (jar label note). Original SU 7922 apparently lost); USNM 124968 (3), coll. C. Rutter, shore, 8-10 June 1903. Shumagin Islands, Chernabura Isld.: BC 63-334 (1), 54°37′N, 162°21′W, intertidal zone, 15-17 July 1958. Aleutian Islands, Tigalda Isl.: BC 63-1311 (5), 54°07′N, 164°58′W, intertidal zone, 28 June 1960. Amak Isl.: BC 65-142 (1), 55°25′N, 163°08′W, tidepool, 9 July 1963; Akutan Isl.: UMMZ 128943 (9), 54°09′N, 165°40′W, shore, 27 July 1939. Unalaska Isl.: UMMZ 106349 (1), vic. 53°50′N, 166°30′W, shore, June 1932; UMMZ 106350 (1), no specifics, 19 June 1932; BC 63-1075 (4), 53°24.5′N, 167°37.0′W, intertidal zone, 23 May 1962; BC 63-1075 (3), 53°23.6′N, 167°32.4′W, intertidal zone, 23 May 1962; USNM 24001 (1), no specifics, coll. W.H. Dall, 20 Jan. 1881; USNM 29826 (2), no specifics, coll. L. Turner, Oct. 1878. Umnak Isl.: BC 63-1068 (7), 52°57.5′N, 168°54.0′W, intertidal zone, 19 May 1962; BC 63-1070 (9) 52°57.5′N, 168°54.0′W, intertidal zone, 21 May 1962; BC 63-1071 (1), same data as preceding; BC 63-1076 (1), 53°25.0′N, 167°50.6′W, intertidal zone, 24 May 1962; UWZ 3553 (1), 52°56.5′N, 167°51.5′W, intertidal zone, 16 June 1962; UWZ 3554 (3), 52°57.8′N, 167°51.8′W, intertidal zone, 18 June 1962; UWZ 3555 (1), 52°58.8′N, 168°51.8′W, intertidal zone, 20 June 1962; UWZ 3556 (3), 53°00.5′N, 168°58.8′W, intertidal zone, 30 June 1962; UWZ 3558 (11), 52°57.5′N, 168°51.5′W, intertidal zone, 17 June 1962; UWZ 3559 (2), 52°56.7′N, 168°52.3′W, intertidal zone, 19 June 1962; UWZ 3560 (2), 52°56.8′N, 168°51.9′W, intertidal zone, 27 July 1962. Adak Isl.: BC 63-1313 (1), 51°45′N, 176°45′W, tidepool, 9 July 1960. Kiska Isl.: BC 63-909 (1), 51°58′W, 177°34′E, intertidal zone, 21 June 1961. Attu Isl.: USNM 117954 (2) Albatross shore coll., 10-11 June 1906. Agattu Isl.: BC 65-9 (1), 52°27′N, 173°30′E, intertidal zone, 26 July 1964; BC 65-14 (1), 52°28′N, 173°35′E, intertidal zone, 29 July 1964; BC 65-20 (5), 52°30′N, 173°37′E, intertidal zone, 2 August 1964.

USSR; Commander Islands; Mednyy (Copper) Isl.: USNM 33870 (1) and 33885 (1), shore coll. L. Stejneger and N. Grebnitski, spring 1883; USNM 33897 (1) and 33901 (1), shore coll., Stejneger and Grebnitski, 6 May 1882; USNM 92590 (1), from ZIL 23948 (holotype of *Commandorella popovi*); USNM 150564 (2), Albatross shore coll., 13 June 1906. Kurile Islands; Shimushir Isl.: USNM 117953 (10), vic. 46°40′N, 151°50′E, Albatross shore coll., 23 June 1906.

Gymnelus popovi. Specimens without data and questionable records: USNM 117918 (8), Attu Island, Aleutian Islands: Albatross Sta. 4784, 247 m (probable label switching); ZIL 23943 (1 of 3), Laptev Sea, 75°17′N, 113°50′E (probable label switching); UW 3425 (1), Bering Sea, Albatross cr. 1890-91.

Gymnelopsis ochotensis (Popov, 1931)

JAPAN; off Iwanai: USNM 117956 (1), 43°00′N, 140°10.5′E, 713-783 m, 19 Sept. 1906; off Niigata: USNM 117939 (1), 38°35′N, 138°41′E, 366 m, 18 July 1906; off Sado Isl.: USNM 117958 (1), 38°08.9′N, 138°31.5′E, 412 m, 19 July 1906, USNM 150067 (1), same data as preceding; Toyama Bay, off Namerikawa: UMMZ 202549 (1), Aug. 1924 (gift to C.L. Hubbs, Aug. 1929); UMMZ 202550 (2), same data as preceding.
USSR; Peter the Great Bay: ZIL 34747 (1), 12 June 1932.
Gymnelopsis ochotensis. No data: ZIL, uncat. (1, 195 mm SL), det. A.P. Andriashev.

Gymnelopsis ocellatus Soldatov

USSR; Okhotsk Sea: USNM 92588 (1), 54°14′N, 143°45′E, 146 m, 12 July 1918; ZIL 23953 (1), same data as preceding; ZIL 32621 (1), same data as USNM 92588; ZIL 23949 (1), 57°47′N, 141°42′E, 150 m, 24 July 1911 (type of *Gymnelopsis guntheri* Popov, ms); ZIL 43289 (1), off Sakhalin Isl., no other data.

Osteological observations were made on the following cleared and stained specimens. Sizes are standard lengths.
Gymnelus viridis. ZMUC 8 (215 mm); NMC 62-410 (112 mm); NMC 77-1259 (4; 193, 150, 127, 116 mm); NMC 62-379 (5; 159, 151, 124, 118, 60 mm); NMC 60-54-S (67 mm); USNM 177574 (110 mm).
Gymnelus retrodorsalis: ZMUC 208 (170 mm).
Gymnelus hemifasciatus: NMC 75-164 (105 mm).
Gymnelus popovi: UWZ 3558 (3; 100, 82, 55 mm).
Gymnelopsis ochotensis: UMMZ 202550: (252 mm); USNM 117956 (222 mm).
Davidijordania poecilimon: UMMZ 202551 (135 mm), Japan, Toyama Bay, 12-13 Aug. 1929, C.L. Hubbs; UMMZ 202552 (106 mm), Toyama Bay, 11-12 Aug. 1929, C.L. Hubbs.
Lycozoarces regani: USNM 105219 (152 mm). Okhotsk Sea, 20 Aug. 1935, A. Ya. Taranets.

Osteological observations were made from radiographs or superficial dissections of a representative sample of all *Gymnelus* and *Gymnelopsis* species plus the following:
Bilabria ornata: ZIL 13089 (1), Okhotsk Sea, Aniva Bay, 28 Aug. 1901, coll. P. Yu. Shmidt; ZIL 42281 (1), Okhotsk Sea; ZIL 43977 (2), Okhotsk Sea, Aniva Bay, 57 m, 21 Nov. 1977.
Davidijordania jordaniana: USNM 92585 (118 mm), Okhotsk Sea, R/V Okhotsk sta. 9, 1912.
Hadropareia middendorffi: ZIL 20147 (3; 219-238 mm), Okhotsk Sea, intertidal zone, Shantar Islands, 18 July 1911.
Hadropareia sp.: ZIL 35815 (2; 134-138 mm), Okhotsk Sea.
Krusensterniella multispinosa: USNM 92592 (125 mm), Okhotsk Sea, 59°12′N, 144°37′E, ca. 110 m, 21 July 1911.
Krusensterniella notabilis: USNM 92591 (syntype, out of ZIL 13011, 109 mm), Okhotsk Sea, off northeast coast of Sakhalin Isl., 55-90 m 1899.
Lycozoarces regani: MCZ 34239 (106 mm), Okhotsk Sea, off Cape Elizaveta, northeast Sakhalin Isl., 8 Sept. 1932; ZIL 26655 (1; 163 mm) Okhotsk Sea, 54°14′N, 143°45′E, 12 July 1918; ZIL 42229 (2; 160, 178 mm), Okhotsk Sea.
Exechodontes daidaleus: VIMS 05406 (100 mm), off Florida, 29°20.5′N, 80°06.1′W, 3 Feb. 1976, 326 m.